THE GENUS RHEXIA (MELASTOMATACEAE)

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The recent and capable revision of *Rhexia* done by Dr. C. W. James (1956) precludes any necessity for extensive reiteration here of the morphology or nomenclatural history of these North American melastomes. However, since that work was done much more information about the genus has been obtained as a result of cytological-anatomical research together with some additional field observations and collections. These, including as they do an additional, well-marked, species and a more intensive field survey of the genus, point toward some emendation.

As James (l.c.) has stated, *Rhexia* is exclusively North American with its greatest concentration of species in the southeastern part of the coastal plain of the U.S.A. Only one (*R. virginica*) extends north as far as Canada; only one (*R. cubensis*) ranges south beyond the United States. Thus, from the standpoint of U.S. botanists, it is a most accessible genus. Fourteen taxa are recognized by James.

The habitat of most *Rhexia* is boggy, a majority of the species being found in such poorly drained areas as bogs, pine flatwoods, savannas, and peaty ditches, invariably on acid, usually sandy, substrates. A majority of species is weedy, coming in rapidly after soil disturbance, burning, logging, etc., and usually being winnowed out by subsequent successional pressures.

The observations made by James and prior authors provide a practical morphological basis for a sectional treatment of the genus, namely that on a basis of pollination mechanism, intergradation, and ecological amplitude, two clearly marked series (A and B) appear to exist. *Rhexia nuttallii*, *R. petiolata* and *R. lutea*, comprising the former series, have short, straight, ascending anthers, show no tendency to cross-pollinate or at least do not produce successful hybrids, tend to have strikingly uniform morphologies over their range, and are less weedy. On the other hand most of the latter series (with the exception of *R. parviflora* and *R. alifanus*) do produce successful hybrids, show considerable diversity of morphology over their ranges, and are often weedy. This latter series is therefore the most problematic. Many of the species are rhizomatous or show a combination of rhizomes and tubers. (Population studies of these are fraught with difficulty in that such species can form clones of enormous extent by means of extensive underground systems so that what at first appears to be a large, rather uniform, population may actually comprise but a few plants.) James recognized nine species (*R. alifanus*, *R. aristosa*, *R. cubensis*, *R. interior*, *R. mariana* var. *mariana* and var. *exalbida*, *R. nashii*, *R. parviflora*, *R. ventricosa*, and *R. virginica*) as making up series B, but had reservations regarding the position of *R. alifanus* within this assemblage.

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Our own, more recent, work has involved some change in approach to the taxonomy of the genus, particularly as to the following:

(1.) On a basis of chromatographic and anatomical analysis of plant parts it would appear that *R. lutea* in series "A" and *R. alifanus* in series "B" of James may actually represent distinct sections.

(2.) Field observations of the species bear out what James discovered regarding hybridization between the Rhexias of series B, but also indicate that a greater degree of hybridization is going on than was formerly recognized. This is supported by collection of F-1's and backcrosses from hybrid swarms, by cytological investigation of species, and by breeding studies of species. Further discussion of these phenomena will follow.

(3.) The complex of forms which either make up or relate to *R. mariana* appears to require a different circumscription. It is recognized that *R. mariana* var. *mariana* is difficult to distinguish either from *R. interior* (*sensu* James) or *R. ventricosa* (*sensu* James). These latter entities differ very little in overall morphology; were their ranges contiguous they would doubtless be considered as one unit. Both have resemblances in their wide leaves and subequal stem faces to *R. virginica* as well but are "marianalike" in their exclusively rhizomatous habit as well as in their character of hypanthium and seed. Both are weedier than *R. virginica*; both hybridise with *R. virginica* as well as with *R. mariana* but hybrids with the former show poor development of seed and capsule while hybrids with the latter do not. The frequency in collections of *R. mariana-R. ventricosa* and *R. mariana-R. interior* intermediates together with the high proportion of seed produced in the capsules of such specimens therefore point to a varietal relationship between all these taxa. (In fact, in that hybrids of *R. nashii* and *R. virginica* show a far greater degree of vigour than do those of *R. mariana* and *R. virginica*, it is reasonable to propose that *R. nashii* actually is more closely related to *R. virginica* than is *R. mariana*.)

A different sort of problem arises when one considers *Rhexia mariana* var. *exalbida* (*sensu* James, Michaux, etc.). The most characteristic form of this entity is a low, slender-rhizomatous, white-flowered, narrow-leaved plant which is hirsute save for the small, sparsely-hairy to smooth hypanthium. Populations of this kind are not uncommon in a region extending from northern Florida northeastward in the coastal plain into eastern North Carolina and as James points out such extremes might well tempt one to treat them as a distinct species (as in fact did Walter, 1788). However, all of the abovenoted characteristics appear to vary independently of each other over the stated range of the entity. For example white-flowered, hairy-hypanthiumed, broad-leaved populations are common in southern Mississippi and southeastern Louisiana; rose-flowered, smoothish-hypanthiumed, narrow-leaved populations are the rule in peninsular Florida; narrow-leaved, larger hypanthiumed, pale-lavender flowered individuals are common in the northeastern part of the range of *R. mariana*. Because of the abovementioned and very demonstrable extremes from within the stated range of *R. mariana* var. *ex-*

albida we have found it difficult to assign even the rank of variety to this assemblage.

In the case of Jame's *R. virginica* var. *purshii* we have also encountered much difficulty in determining its relationship to *R. virginica* proper and find it impossible to delimit this variety in any way useful to a systematic treatment.

(4.) Therefore, on the basis of the abovementioned observations we present a new treatment of *Rhexia*, also incorporating into this a new species of *Rhexia*, *R. salicifolia*, first discovered by Dr. R. K. Godfrey in northern Florida during late summer of 1961. We treat a total of thirteen taxa (including two varieties).

The authors of this paper undertook its first stages independently, but they concur as to what comprise the taxa of *Rhexia* and also are agreed that a combination of their work would enhance the effectiveness and utility of a taxonomic treatment. We base our opinions on greenhouse observations, anatomical studies, breeding experiments (still being continued), cytological evidence, and field experience with *Rhexia* over an area extending from New Jersey south into Florida and west to the limits of the genus in Texas. Over 900 numbers of *Rhexia* have been added to collections as a result; over 2500 duplicates are being distributed to the following herbaria: ALU, C, DS, ENCB, FSU, GH, ILL, KANU, LL, MICH, MISSA, MSC, NCU, NY, P, PH, RSA, SMU, TEX, UC, US, VPI, VT, WIS. Duplicates of most of these numbers are deposited at VDB; vouchers for cytological, anatomical or chromatographic studies are deposited at NCU and/or GEO.

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We wish also to thank curators and staffs of the following institutions for their kindness in providing loans of *Rhexia* for study (abbreviations in accordance with J. Lanjouw and F. A. Stafleu, 1964): DUKE, the Herbarium of Duke University, Durham, North Carolina; FSU, the Herbarium of the Department of Biological Sciences, Florida State University, Tallahassee; NCU, the Herbarium, Department of Botany, University of North Carolina, Chapel Hill; SMU, the Herbarium, Southern Methodist University, Dallas, Texas.

The Latin diagnosis of *Rhexia salicifolia*, sp. nov., was written by Dr. L. H. Shinners.

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The junior author's contributions to this paper are from a thesis submitted

to the Graduate School of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the Ph.D. degree in Botany. The study was done under the direction of Dr. C. Ritchie Bell. Financial assistance for the junior author was furnished by a National Science Foundation Cooperative Fellowship.

MORPHOLOGY AND ANATOMY

Habit. All *Rhexia* are perennial, their erect or ascending shoots arising annually from erect, subligneous caudices or from slender to stout, horizontally spreading, rhizomes. Perennation is from lateral buds, arising in a rather random fashion from the crown or from the rhizomes; in some species tubers are produced in addition, these usually of a short-oblong or fusiform shape similar to small sweet potatoes. Development from seed is fairly rapid, most of the species reaching flowering size (in greenhouse) within a year. *Rhexia alifanus* and *R. lutea* are exceptional, perhaps because of the additional time required for the seedlings to put down very lengthy taproots. Seedling flats of both seemed to stagnate in the flats while the seedlings of other species were putting on considerable height growth. Later, when the root systems of the former two species were examined it was noticed that the taproots had already reached the bottom of the shallow flats. When these particular seedlings were released by potting them separately in deep clay pots the growth response was both rapid and profuse; however, it is still probably likely that both *R. lutea* and *R. alifanus* do not bloom until the second year and this is also very often the case in nature with the other species as well. No stratification is necessary for abundant seed germination, seed of all species germinating in the greenhouse at any time of year. In nature most germination is probably in the spring, and therefore a period of after ripening may be required. This has not been tested.

Stems. The stems of *Rhexia* toward the base tend to be terete, and in many cases with a development of shreds of corky tissue. In very wet situations the stem bases may become quite thickened and spongy (this is especially noticeable in such wet-ground species as *R. virginica* and *R. aristosa*). Toward the midstem and up to the level of the inflorescence the axis becomes angulate. In *R. aristosa*, *R. mariana* var. *interior*, *R. mariana* var. *ventricosa*, and *R. salicifolia* there are four subequal stem faces; in the former two species the margins of the sessile leaves appear to be decurrent the length of the internode as narrow wings. In the other species of *Rhexia* one pair of stem faces is narrower and concave, the other slightly convex and broader. The two contrasting stem types are best displayed at mid-stem. The stem anatomy is typical of melastomes (Metcalfe and Chalk, 1950). All taxa of the genus have internal or intraxylary phloem. The pith is usually relatively large and is composed of large parenchyma cells. The crystal aggregates so common in the leaves of some taxa are also found in the pith and in the epidermis of the stem. These crystal aggregates are apparently confined to parenchymatous tissues. Stem wings, when present, are always vascularized and the number of vascular bundles seems to depend upon the

degree of development of the stem wings. The interspecific variations in stem structure of the genus are not sharp enough to be useful in the classification of the various taxa comprising the genus.

Leaf arrangement. Leaf arrangement in *Rhexia* is decussate; each pair of opposing leaves is in a plane perpendicular to that occupied by those of adjacent nodes. In *Rhexia* the leaves are either sessile or short-petiolate, with petiole length greatest at the lower nodes of a stem.

Leaves. Leaves of *Rhexia* are simple and in most species three-nerved. In *Rhexia virginica* there may be more than three and in *R. mariana* var. *mariana*, *R. cubensis* and *R. salicifolia* the central nerve only may be conspicuous. In those species with lateral nerves, the nerves are arcuate. The margins may range from subentire to distantly or approximately serrulate, the tips of the very low, ascending teeth often drawn out into fine, gland-tipped, multicellular trichomes. Surfaces of leaves may range from glabrous to hirsute or glandular hairy. Orientation of leaves ranges from slightly recurved to horizontal or sharply ascending. The blades in all species save *R. salicifolia* are situated so that the flat side faces the axis of the plant; in *R. salicifolia* the blades are in a plane perpendicular to the ground, hence the edges of the leaves face the axis. In *R. lutea*, *R. petiolata*, *R. nuttallii*, *R. mariana*, *R. nashii* and *R. virginica* the stomata are concentrated on the lower surface of the blade; in *R. cubensis*, *R. aristosa*, *R. parviflora*, *R. salicifolia*, and *R. alifanus* the stomata are frequent on both surfaces. Stomata of *Rhexia* are ranunculaceous or anisocytic; i.e., they are surrounded by ordinary epidermal cells, usually three in number. *Rhexia alifanus* appears to be significantly different in its stomate density. The mean stomate density for plants of this species (lower epidermis) is 235 per square millimeter, while the average mean density for the remaining taxa is 882. The taxon with the next highest density is *R. salicifolia* with a density of 529. It may be significant that both of these species are xerophytes and that both have stomata on both leaf surfaces.

In its cross-sectional pattern, *Rhexia alifanus* stands out from the other species of the genus because of its peculiar leaves, which are isofacial, i.e., the upper and lower surfaces are indistinguishable except by their orientation to the axis of the plant. The internal structure, except for the vascular tissue is bilaterally symmetrical, both transversely and longitudinally. The palisade mesophyll is biseriate. Each of the two palisade mesophylls consists of two layers of typically "sausage-shaped" cells. A thin spongy mesophyll separates the two palisade layers. Although *R. alifanus* is not the only species with two separate palisade mesophylls, it is the only species in which the internal structure is so symmetrical and in which there are two double palisade layers. This, and other features of the leaf of this species, such as the greatly developed waxy cuticle and the vertical orientation of the leaves, is probably a xeromorphic modification. *R. alifanus* occupies some of the driest habitats of all the species of *Rhexia*, often being found on extremely dry sands or sandy peats. A biseriate palisade mesophyll (two

layers separated by a spongy layer) is also present in the leaves of *Rhexia aristosa* and *R. salicifolia*. These two species, especially the latter, can also occupy xeric sites, and in both, the leaves tend to be vertically oriented.

The leaves of all species of *Rhexia*, except those of *R. alifanus*, are bilaterally symmetrical in the longitudinal plane. Unlike *R. alifanus* the leaves of the other species develop some degree of folding, which may vary from the nearly flat leaves of *R. nuttallii* to the typical V-shape (in cross-section) of the leaves of *R. cubensis* and some populations of *R. mariana*. However, in most cases, the degree of folding is probably due to diurnal and seasonal changes in temperature, relative humidity, illumination, and other environmental factors. The age of the leaf probably also affects the degree of folding. It may be said, however, that the leaves of *Rhexia alifanus* are always flattened and that the leaves of the remaining taxa exhibit varying degrees of folding.

Holm (1907), Solreder (1908), and Metcalfe and Chalk (1950) have reported the presence of crystal aggregates of calcium oxalate in various organs of members of the Melastomataceae. Holm reported their presence in the leaves and stem of *Rhexia virginica* and their absence in the same organs of *R. mariana*. The crystal aggregates, when present, are located in the spongy mesophyll of the leaf and in the epidermis, wings, and pith of the stem. In the leaf, the crystals are associated with vein endings, but in *R. aristosa* there is a much greater concentration of crystal aggregates along the main vein than in other areas of the leaf. Crystal aggregates are present in *R. nuttallii*, *R. alifanus*, *R. aristosa*, *R. nashii*, *R. mariana* (but not in all populations), *R. mariana* var. *interior*, *R. mariana* var. *ventricosa*, *R. virginica*, and *R. salicifolia*. They are absent in the other species and in some populations of *R. mariana*.

Inflorescence. The inflorescence of *Rhexia* is cymose, fundamentally a simple or compound dichasium. It is most greatly reduced in *R. petiolata* and *R. nuttallii*, in which the flowers may actually be solitary and ranges (this usually based on the vigour of the plant) to a diffuse system. Branching within such a system is often dichotomous, two lateral branches developing at the base of each central flower and these in turn terminating in a simple dichasium of three flowers or again branching. In some examples the inner branches of a particular dichotomy may abort or be reduced, hence parts of the inflorescence may assume a secund-racemose aspect (see illustrations). Bracts arise from most of the nodes of the inflorescence, the lowermost of these resembling upper stem leaves, the ones directly subtending flowers often much reduced or even scale-like (in the case of *R. alifanus* they are scale-like and early deciduous).

Flowers. The flowers of *Rhexia* are, save for the androecium, actinomorphic, either subsessile or at least produced on pedicels shorter than the calyx. According to Eyde and Teeri (1967) who made detailed observations of the floral anatomy of *R. virginica*, the tissues of the prominent hypanthium are fused to all but the uppermost (beaked) portion of the ovary wall, hence the ovary is definitely inferior. This is in agreement with the observations

of Fernald (1950) and James (l.c.) but not with those made by Gleason and Cronquist (1963). The cause for such conflicting observations, Eyde and Teeri state, is the fact that during maturation of the fruit cell layers in the fruit wall separate prior to dehiscence so that the partly inferior ovary appears superior. The hypanthium itself is oblong-cylindrical in the bud becoming flask-shaped at maturity, being divided into a tubular neck, from which the four calyx lobes spread and a globose or subglobose body which itself encloses the capsule. The calyx lobes range from broadly to narrowly triangular and are usually spreading at time of anthesis and on the fruiting hypanthium.

The four petals of *Rhexia* are convolute in the bud, when expanded broadly oblong, obovate, or even suborbicular, the bases oblique. Venation of the petals is delicate but distinct, the larger veins several, simple and slightly spreading at the petal base, finely branched distally. If one takes a "face-on" view of a flower it is seen that the central vein of a petal extends more or less diagonally across the broad blade, and is usually excurrent as a short to quite prominent slender trichome. Hence, because the blade itself is asymmetric, the midvein does not bisect it. The side of the blade to the left of the midnerve has much less area and is more gently curved than is the side of the blade to the right which is much more strongly curved, particularly distally, and the apex of which comprises most of the petal tip. In some species of *Rhexia* (e.g. *R. nashii*) a portion of the petal back is trichomiferous; such trichomes appear on that part of the corolla that is exposed in the bud, that part correlating with the narrower, "left" hand, portion of the blade. In all *Rhexia* the petals are fairly quickly deciduous, those of *R. nuttallii*, *R. petiolata* and *R. lutea* lasting not much more than a day and those of the remainder of the species usually expanding in the early hours of the morning and being shed by afternoon. In *R. nuttallii*, *R. lutea* and *R. petiolata* the expanded, upper surface of the petal blade is concave and the petals at anthesis are curved tongue-like and also somewhat ascending; in the rest of the species the petals at anthesis spread horizontally from the hypanthium and are plane.

Anthers. According to James and Eyde and Teeri (l.c.) the eight stamens of *Rhexia* in the bud are bent inward with their tips inserted into shallow pockets around the upper part of the ovary. The anthers as anthesis approaches are twisted on their filaments in a counterclockwise fashion, all being brought into a roughly parallel position toward the lower part of the open flower and with their apices directed outward and downward. The anther itself is four-locular in its early stages of development, but through a breakdown of the septa it becomes unilocular at anthesis; pollen is shed through a solitary, circular, apical pore.

Gynoecium and fruit. The gynoecium of *Rhexia* is comprised of a mostly inferior, four-locular ovary tipped by a single linear style. The stigma is truncate. The placentation of the numerous ovules is axile. The fruit, which develops is a loculicidal capsule which remains enclosed within the hypanthial body.

Seed. All species but *R. alifanus* have cochleate seed whose surfaces are marked with concentrically oriented, regular or irregular ridges of tubercles, papillae or laterally-flattened, domelike projections. The seed of *R. alifanus* is itself larger, roughly triangular in outline with a smoothish surface. Sculpturing of seed of many of the species, particularly *R. mariana* var. *mariana R. nashii*, and *R. virginica* is quite variable. Our own drawings are merely attempts to portray some of the commoner forms of sculpture; thus, in regard to seed, drawings have great limitations.

CYTOLOGY

1. *Chromosome numbers.* Chromosome preparations of all *Rhexia* species were made by fixing buds in the field in 3 absolute ethanol: 1 glacial acetic acid. Microspore parent cells were observed by squashing and staining with aceto-carmine. Voucher specimens are deposited in the following herbaria: EU, NCU, and VDB.

The base or "X" chromosome number for the genus *Rhexia* is eleven. No departures from this base number or multiples thereof were observed. Chromosome counts were consistent within a population. All cells observed from plants of the same species population had the same number of chromosomes. In several taxa, the number varied from population to population (polyploidy). No meiotic irregularities were observed in any of the preparations.

Chromosome counts for plants of the various *Rhexia* taxa are presented in Table I.

There are polyploid series in *R. cubensis*, *R. nashii*, *R. mariana*, and *R. virginica*; and there are polyploid taxa without any extant or known diploid relatives within those taxa (*R. lutea*, *R. nashii*). All ploidy levels in *R. cubensis* were found within a three county area on the Florida panhandle.

No morphological differences could be detected between diploid and polyploid plants of any of the taxa, although there were often slight chromatographic differences.

The chromosome number of *Rhexia alifanus* is not distinctive, but the size of the chromosomes is. As previously figured (Bostick, 1965), the metaphase chromosomes of *R. alifanus* are much larger than the metaphase chromosomes of *R. mariana*. This is also true when the chromosomes of *R. alifanus* are compared to those of the other taxa of the genus.

2. *Pollen.* Pollen from dried specimens was used in the study of pollen morphology and size. Pollen from a single anther from each population studied was scraped onto a slide, drenched with absolute ethanol and mounted in methylene blue in glycerine jelly. One hundred grains from each population were measured. Scores of pollen size of five populations of each taxon were combined (with the exception of *R. parviflora*, where only two populations were sampled).

The tetrad arrangement in all taxa of the genus is of the tetrahedral system. The pollen grains' morphology is consistent with that described for the Melastomataceae by Erdtman (1952) in that the grains are spheroidal and

TABLE I

CHROMOSOME NUMBERS IN *RHEXIA*.

Unless otherwise stated, collection numbers are those of the junior author. Localities are given by county and state.

Taxon	*n*	*Collection no. and locality*
R. petiolata Walt.	11	332-1, Duplin, N.C.; 343-2, Brantley, Ga.; 346-2, Clay, Fla.; 372-3, Franklin, Fla.; 359-1, Hillsborough, Fla.
R. nuttallii James	11	343-1, Brantley, Ga.; 348-2, Clay, Fla.; 353-2, Indian River, Fla.; 396-1, Walton, Fla.
R. lutea Walt.	22	412-2, Lee, N.C.; 392-2, Franklin, Fla.; 378-1, Jackson, Miss.
R. salicifolia K & B	11	400-1, Bay, Fla.; 398-2, Walton, Fla.
R. parviflora Chapm.	11	391-1, Franklin, Fla.; 393-1, Franklin, Fla.
R. aristosa Britt.	11	185-1, Princess Anne, Va.; 337-1, Bladen, N.C.; 384-1, Barbour, Ala.
R. virginica L.	11	338-1, Bladen, N.C.; 439-1, Wilson, N.C.; Clark 1953, Marion, Tenn.; 403-3, Clinch, Ga.; 342-2, Wayne, Ga.; 346-3, Clay, Fla.
	22	331-1, Duplin, N.C.; 435-1, Wake, N.C.; 418-1, Fayette, Tenn.; 374-2, Tuscaloosa, Ala.; 377-2, Choctaw, Ala.; 342-1, Wayne, Ga.; 346-2, Clay, Fla.
R. mariana L. var. *interior* (Pennell) Kral & Bostick	22	417-1, Hardeman, Tenn.; 424-1, Benton, Ark.
R. mariana L. var. *ventricosa* (Fern. & *Grisc.*) Kral & Bostick	22	444-1, Dinwiddie, Va.; 443-1, Nash, N.C.; 438-1, Wilson, N.C.
R. mariana L.	11	405-2, Jasper, S.C.; 341-1, Long, Ga.; 386-2, Miller, Ga.; 389-1, Franklin, Fla.; 359-1, Hardee, Fla.; 399-1, Walton, Fla.; 380-1, Morehouse, La.; 421-1, White, Ark.; 422-1, Faulkner, Ark.
R. cubensis Griseb.	11	350-1, Putnam, Fla.; 368-3, Franklin, Fla.
	22	388-1, Franklin, Fla.
	33	406-1, Berkeley, S.C.; 395-1, Bay, Fla.; 398-1, Walton, Fla.
R. nashii Small	22	180-1, Harnett, N.C.; 329-1, Orange, N.C.; Wilson, N.C.; 345-1, Union, Fla.
	33	330-1, Duplin, N.C.; 369-1, Franklin, Fla.; 356-1, Highlands, Fla.
R. alifanus Walt.	11	412-3, Lee, N.C.; 123-5, Bladen, N.C.; 405-1, Jasper, S.C.; 387-1, Grady, Ga.; 346-1, Clay, Fla.; 392-1, Franklin, Fla.

tricolpate with three additional pseudocolpi. The colpi in *Rhexia* and in the other members of the family each contains a single germinal pore. The exine is characterized by the presence of six darkly-staining, thickened ridges which are adjacent to each colpus and pseudocolpus. Pollen morphology is the same in all taxa of the genus; and the only interspecific difference to be found in the pollen grains is in their diameters.

The pollen size range for the entire genus is quite narrow (16-33 micra); and the interspecific differences are so narrow that no species may be separated from any of the others on the basis of pollen grain diameter. There is a rather vague correlation between ploidy level and pollen grain diameter. Polyploids tend to have the largest pollen, although this trend is weakened by the relatively small pollen of the tetraploids of *Rhexia lutea*, *R. nashii*, and *R. mariana*. It is to be expected that there should be a correlation between ploidy level and cell size, since an increase in chromatin should be accompanied by an increase in cytoplasm with a corresponding increase in cell volume.

TAXONOMIC TREATMENT

Some special problems in identification of Rhexia. The treatment which follows should be used with the following qualifications:

(1.) In this treatment, as in preceding treatments, much use is made of relative width and character of the pairs of stem faces. As was already mentioned there is one group made up of such taxa as *R. virginica*, *R. mariana* var. *interior*, *R. mariana* var. *ventricosa*, *R. parviflora*, *R. salicifolia*, and *R. aristosa* in which the faces at mid-stem are subequal while in the rest of the species one pair of stem faces is narrower and concave, the other slightly convex and broader. This difference, however real, is hardest to apply to herbarium material where some stem character is lost through pressing of the specimens. In fact, identification becomes involved with gaining, through experience of examining many specimens, a concept of the relative "squareness" or "roundness" of the stem in cross section. This contrasting character is best observed in the middle and upper internodes of the main axis of a stem.

(2.) Shape of the mature hypanthium is a critical diagnostic feature of *Rhexia* species. Of particular importance is the length of the body of the hypanthium in relation to the length of the hypanthial neck. Total length of hypanthium in our work is a measure from the point of attachment of pedicel to body to hypanthial rim. Thus the length of the calyx lobes is not included. The body of the *Rhexia* hypanthium is usually globose, but can range to ovoid or depressed-globose. In any event, the shape of the hypanthial body is determined, its length measured, and a measurement is taken from the tip of this body outline to the rim of the hypanthium in order to get the neck length. The neck of the hypanthium is definitely longer than the body in *R. aristosa*, *R. nashii*, *R. cubensis*, *R. mariana* var. *ventricosa*, *R. mariana* var. *interior*; usually it is shorter than the body in *R. virginica*, *R. salicifolia*, southern forms of *R. mariana* var. *mariana*, *R. nuttallii*, *R.*

lutea, *R. petiolata*, *R. parviflora*. It is quite variable in northern and western forms of *R. mariana* var. *mariana*.

(3.) Unless otherwise indicated, leaf characters are drawn from mid-cauline leaves.

RHEXIA L., Sp. Pl. 346. 1753.

Alifanus Pluk. ex Adans. Fam. Pl. 2: 234. 1763.

Erect, sometimes woody-based, perennial herbs from woody, ascending caudices, narrow rhizomes, or tubers or a combination of rhizomes and tubers. Stems hirsute and/or glandular-hairy (except for *R. alifanus*), usually 4-angled above the thickened woody base, the angles in some species winged. Leaves opposite, decussate, usually with three main veins, the venation arcuate, petiolate or sessile, the margins serrate or serrate and ciliate, the apices characteristically acute. Inflorescence cymose, the flowers few to many, slightly zygomorphic. Bracts consistent with the shape of the leaves but much smaller, often deciduous. Receptacle elevated, forming with the perianth base a two-layered, urceolate, hypanthium the inner layer of which bears stamens and petals at its tubular apex with the outer layer producing triangular calyx lobes. Sepals four, the calyx lobes usually narrowly triangular, flaring or ascending, acute or aristate. Petals four, distinct, the blades asymmetrical, oblique, ascending, or horizontally spreading at anthesis, lavender, pink, white or (in one species) yellow, broad, convolute in the bud, the apices broadly rounded or truncate, and with the mid-vein excurrent as a slender multicellular hair, the margins entire, the bases short-clawed, the surfaces smooth above, but in some species bearing glandular hairs beneath on that area exposed in the bud. Stamens eight, subequal, in two whorls; anthers 1-celled at anthesis, basifixed, introrse, usually well-exserted and declined toward the base of the opened flower, also oriented in a parallel fashion, yellow, linear-oblong to linear-lanceolate; dehiscence through a terminal, adaxial, pore; filament long, slender, pale, downwardly curved, with a small protuberance or hook-like appendage at its point of juncture with the anther. Carpels four, fused into a four-locular gynoecium which terminates in a single, slightly sigmoid or curved, button-tipped, style. Placentation axile, the ovules numerous, on massive placenta. Fruit capsular, enveloped closely by the hypanthial body, and with a loculicidal, somewhat irregular, dehiscence. Seeds curvate, commonly cochleate (shaped like a snail shell), small. Seed coat pebbled, ridged, tubercled or smooth.

A genus common to moist, acid, sandy or peaty situations such as bogs, ditches, savannas and pine flatwoods, centering in the southeastern United States but extending as one species north into eastern Canada and as one species southward into the Caribbean islands.

Type species: *Rhexia virginica* L.

A KEY TO RHEXIA

1. Plants with woody, stout, ascending caudices or taproots; anthers short, at anthesis seldom longer than 2 mm., almost straight; petals at anthesis

ascending, definitely not horizontally spreading or plane.

2. Leaves predominently of an ovate type; plants sparingly branched; internodes smooth; flowers, later fruit, partly concealed by closely subtending bracts similar in shape to stem leaves and but little smaller; mid-portion of stems angled.
   3. Teeth of leaf margins at mid-leaf usually drawn out into hairs 1 mm. long or slightly longer; sepal lobes acuminate-aristate; hypanthium smooth save for a few hairs at and between the sepal tips; seed with a pebbled surface . . . . . 1. *R. petiolata* Walt.
   3. Teeth of leaf margins at mid-leaf blunt or, if terminating in a hair, the hair shorter than 1 mm.; mid-portion of stems flattened or ridged but not angled; hypanthium glandular-hairy, the sepal tips blunt or acute, but definitely not acuminate; seed ridged, 2. *R. nuttallii* James
2. Leaves predominantly of an oblong, linear or spatulate type; plants usually bushy; petals yellow, the flowers and fruit not concealed as above; internodes with at least a scattering of hairs. 3. *R. lutea* Walt.

1. Plants with various types of rootstocks but anthers longer, curvate; petals at anthesis horizontally spreading, plane.
   4. Stems with at least some hairs at the nodes, usually the internodes also hairy; seed cochleate (shaped like a snailshell).
      5. All 4 stem faces at mid-stem approximately equal, the stem faces almost flat, the angles sharp or winged.
         6. Leaves predominantly of a linear, spatulate, oblong or elliptical type, the blades turned to a vertical position; neck of hypanthium shorter than the body; the plants tuberiferous, rhizomatous, or both; plants of sandy margins of limesink lakes, n.w. Florida. . . . . 4. *R. salicifolia* Kral & Bostick
         6. Leaves predominantly of a lanceolate, elliptic or ovate type, the blades not oriented as above; neck of hypanthium shorter or longer than body; plants tuberiferous or rhizomatous or both, of more general distribution.
            7. Petals white; hypanthium smoothish, usually 5-7 mm. long; leaf blades at mid-stem pronouncedly petiolate; diminutive short-rhizomatous plants of swamp margins, Franklin Co., Florida. . . . . 5. *R. parviflora* Chapm.
            7. Petals lavender to lavender-rose; leaf blades at mid-stem subsessile or short petiolate; tuberiferous plants of wider range.
               8. Stem angles conspicuously winged at mid-stem; lower portion of stem usually thickened, sometime spongy; hypanthial neck rarely longer than body of hypanthium.
                  9. Hypanthial lobes flaring horizontally, aristate; area of hypanthial rim with long, stiff, yellowish, tapering, flaring trichomes; petals dull lavender . . 6. *R. aristosa* Britton
                  9. Hypanthial lobes and hairs not as above; petals bright lavender-rose. . . . . 7. *R. virginica* L.

8. Stem angles at mid-stem wingless or very narrowly winged; hypanthial neck usually longer than the body.
   10. The plants strictly rhizomatous, the internodes of stem hirsute; hairs of mature hypanthia scattered rather evenly over the surface; leaf surfaces hairy; lobes of hypanthium not flaring horizontally and not aristate, nor alternating with long, stiffly flaring trichomes; flowers bright lavender-rose.
      11. Seeds papillate, the papillae in concentric lines; plants primarily of eastern seaboard. . 9. *R. mariana* L. var. *ventricosa* (Fern. & Grisc.) Kral & Bostick
      11. Seeds irregularly ridged in concentric lines; plants primarily from west of the Mississippi River or in interior physiographic provinces. . . 10. *R. mariana* L. var. *interior* (Pennell) Kral & Bostick
   10. The plants tuberiferous, the internodes of stem smooth or smoothish; nodes only with tufts of spreading hairs; hairs of mature hypanthium crowded toward its neck and orifice, stiff, flaring, yellowish, some as long as the calyx lobes; lobes of hypanthium aristate, flaring horizontally; flowers large, dull-lavender. . . . . 6. *R. aristosa* Britton
5. All four stem faces not even approximately equal, one pair of opposing faces broader, darker green, convex, the narrower pair paler, concave (thus the stems having a more cylindrical appearance at mid-stem).
   12. Flowers white; lower and mid-cauline leaves ovate to ovate-lanceolate.
      13. Bracts elliptic or broader, often nearly as broad as the hypanthia they subtend, giving mature inflorescence a "leafy" look; petals suborbicular; plants short-rhizomatous; edges of cypress or titi swamps, Franklin Co., Florida. 5. *R. parviflora* Chapm.
      13. Bracts linear or narrowly triangular, definitely narrower than the hypanthia they subtend and giving the mature inflorescence a more naked look; petals narrower; plants long-rhizomatous, usually on drier substrata and of much wider distribution. . . . . 8. *R. mariana* L. var. *mariana*
   12. Flowers white or lavender or rose; lower and mid-cauline leaves linear, oblong, lanceolate or spatulate.
      14. Leaves predominantly of a linear, oblong or spatulate shape; hypanthium at maturity 1 cm. or longer, with a scattering of gland-tipped hairs; plants both rhizomatous and tuberiferous; petals bright lavender-rose; commonly of lower, sandier portions of the Atlantic and Gulf Coastal Plain. . . 11. *R. cubensis* Griseb.
      14. Leaves various, but if leaves linear, the hypanthium shorter, smoother, and the petals smaller.
         15. Hypanthium smooth, 1 cm. long or more at maturity; leaves

at mid-stem predominantly lanceolate or narrowly ovate; plants occasionally tuberiferous, always rhizomatous; exposed petal parts of buds with at least a scattering of glandular hairs; petals large, dull-lavender. . . 12. *R. nashii* Small

15. Hypanthium with at least some hairs, usually shorter; plants exclusively rhizomatous; exposed petal backs of bud smooth; petals smaller, ranging from white to pale lavender, rarely bright lavender. . . . 8. *R. mariana* L. var. *mariana*

4. Stems smooth, even at the nodes; tall, wand-like, bright rose-flowered plants of open pine barrens, the hypanthia usually copiously glandular-hairy; seed wedge-shaped. . . . . 13. *R. alifanus* Walt.

1. RHEXIA PETIOLATA Walt., Fl. Carol. 130. 1788. (Fig. 1, p. 420; map, p. 437.)

Rhexia ciliosa Michx., Fl. Bor.-Am. 1: 221. 1803.

Low, smoothish, perennials from short, stocky, caudices. Shoots solitary or several, 1-5 dm. tall, rigid, sparingly branched or simple, angular, brownish and with a thin, slightly exfoliating bark below, upwardly becoming tan or reddish-brown, smooth or with a few hairs at the nodes. Leaves predominantly ovate to suborbicular, the larger ones 1.0-1.5 cm. long (rarely 2 cm. long), ascending, short-petiolate, the surfaces usually smooth, the apex acute to acuminate or bristle-tipped, the margins serrulate, the ascending tips of the teeth terminating in conspicuous hairs, thus imparting a ciliate look to the blade margin. Basal leaves broadest, usually shorter than those of the mid-stem into which they gradually grade, upwardly gradually grading into the bracteal leaves which are similar in shape and size to upper stem leaves and which usually partly conceal the flower bases, later the fruit. Inflorescence a few-flowered, but generally congested, leafy cyme. Petals slightly asymmetrical, broadly oblong, elliptic or ovate, to 2 cm. long, lavender-rose, glabrous, remaining somewhat involute at anthesis, never horizontally spreading. Anthers ca. 2 mm. long, on filaments up to 4 mm. long, but usually shorter. Mature hypanthium 5-7 (-9) mm. long, smooth save for a few elongate hairs around the rim and on the sepal lobes, the body globose or depressed-globose, abruptly contracting into the short-cylindrical base of the neck which in turn flares into a broadly spreading orifice whose lobes are narrowly triangular-acuminate and which are tipped by elongate tapering yet fairly stiff, hairs. Seeds ca. 0.6 mm. long, cochleate, the surface usually pebbled, or covered with numerous, short ridges of dome-shaped processes.

Moist acid sands and sandy peats of bogs in pine flatwoods, savannas, and rights-of-way, Coastal Plain, southeast Virginia south into peninsular Florida west into eastern Texas. Chromosomes: N equals 11.

Type: "Rhexia 723," Walter Herbarium at BM. James states that the type is fragmentary, but the species can be identified from the type description, however brief.

2. RHEXIA NUTTALLII James, Brittonia 8: 214. figs. 1, 17. 1956. (Fig. 2, p. 421; map, p. 438.)

R. serrulata Nutt., Gen. 1: 243, 1818, non Rich. in Bonpl. Rhex. 74, pl. 28. 1813.

Low, smoothish perennials from short, stocky, caudices. Shoots solitary or several, 1-3 (-4) dm. tall, rigid, sparingly branched or simple, subterete, brownish and with a thin, sometimes exfoliating bark toward the base, upwardly becoming greenish-brown or reddish-brown or tan, usually smooth. Leaves predominantly ovate to suborbicular, the larger ones 1.0-1.5 cm. long, the surfaces smoothish, dark yellow-green above and paler green or maroon beneath, the apex obtuse to acute, the margins subentire to serrulate. Basal leaves broadest and with the longest (to 1.5 mm.) petioles, gradually lengthening toward mid-stem, thence gradually grading into the bracteal leaves which are of similar shape and often nearly as large. Inflorescence a sparse-flowered, usually regular, cyme, with the flowers and young hypanthia partly concealed by subtending bracts. Petals slightly asymmetrical, broadly cuneate or obovate, 1.0-1.2 cm. long, lavender-rose, at anthesis slightly spreading but certainly not flaring horizontally, the blades somewhat involute, the mid-vein excurrent as a short hair, the petal backs with at least some gland-tipped hairs. Mature hypanthium 0.5-0.7 cm. long, glandular-hairy, brownish, almost woody in appearance, on stout pedicels to 3 mm. long, the hypanthial body globose or depressed-globose, abruptly narrowing to a very constricted, short neck with flares into an orifice fully as broad as the hypanthial body; hypanthial lobes deltoid, the tips usually obtuse or blunt. Anthers at anthesis short-linear, about 2 mm. long, straight, on filaments to 3.5 mm. long. Capsule smooth, depressed-globose. Seeds ca. 0.6 mm. long, cochleate, the crest marked with irregular lines of laterally compressed, dome-shaped, processes. Chromosomes: N equals 11.

Sandy peat of pine flatwoods bogs, southern Georgia and throughout Florida.

Type: "Georgia," Baldwin (Nuttall 220). At PH. Isotype at NY seen.

Remarks: This well-marked species is one of the rarest in collections, probably because its small size makes it an insignificant element among other flatwoods plants. However, it is fairly abundant in the pine-saw palmetto flatwoods of peninsular Florida, and shows weedy tendencies on bulldozed, yet still moist sandy soils there. *R. petiolata* Walt. is quite similar to it in habit and flower and is common in the same localities but no natural hybrids between the two have ever been reported.

3. RHEXIA LUTEA Walt., Fl. Carol. 130. 1788. (Fig. 3, p. 432; map, p. 437.)

Stiffly branching perennial, several rigid shoots arising from a thickened, caudex or taproot. Shoots seldom longer than 4 dm., hirsute with spreading hairs, the lower portion of the stem usually reddish-brown, subterete, sometimes developing a thin tight smooth bark, the mid and upper portion of the stem somewhat four-angled (rarely low-winged as well), the intervening faces flat or convex. Leaves (obovate-) spatulate to elliptic or narrowly

oblanceolate, all but the lowermost subsessile, the larger ones 2-3 cm. long, dark yellowish-green above, paler beneath and evidently triple-nerved with the two lateral nerves very close to the margin on narrower leaves; leaf surfaces with slender but stiff, usually appressed, yellowish trichomes; leaf apex acute, obtuse, rounded, or mucronate; leaf margin subentire to, more frequently, distantly low-serrate, the teeth closely ascending, often terminating in slender hairs. Leaves lengthening and narrowing up to the area of mid-stem, thence gradually reducing into the bracts of the inflorescence; leaves of branches of the main axis invariably much shorter and narrower and from shorter internodes. Inflorescence a regularly branched often dichotomous cyme, frequently quite congested and made quite leafy by the persistent bracts. Petals obovate to broadly cuneate, 1.0-1.5 cm. long, yellow, ascending in the flower at anthesis, but definitely not spreading horizontally, smooth save for the hair-like projection of the midvein. Anthers at anthesis short-linear, ca. 2 mm. long on filaments up to 5 mm. long; style at anthesis little longer than the stamens. Mature hypanthium 6-7 mm. long on a stout pedicel 1-2 mm. long; hypanthial body globose, abruptly contracting into a short-cylindrical lower neck which in turn flares into a campanulate upper neck, the whole neck slightly shorter than the body. Sepal lobes narrowly triangular, aristate. Hypanthial hairs long, spreading, usually confined to the neck and to the sepal lobes. Capsule smooth, globose but for a slender apex. Seed cochleate, ca. 0.7 mm. long, with a few straight ridges of papillae along the crest, the sides with lower, more scattered papillae or smoothish. Chromosomes: N equals 22.

Sandy peat or sandy clay peat of pine flatwoods, savannas, hillside seepage areas and bogs, Coastal Plain, eastern North Carolina south into northern Florida and west into eastern Texas.

Neotype: moist ditch near pond with Nyssa, 2.3 mi. w. St. Stephen, Berkeley Co., South Carolina, *James 678.* (At GH).

Remarks: This species, with its unique hypanthial shape and yellow flowers, is too well marked to invite much further comment. Like *R. alifanus*, it shuns lower peninsular Florida. Actually it is most abundant west of Florida in southern Alabama, Mississippi, southern Louisiana and southeastern Texas. There it is often common in *Sarracenia* bogs and savannas.

4. RHEXIA **salicifolia** Kral & Bostick, sp. nov. (Fig. 4, p. 423; map, p. 438.)

Planta humilis (ca. 20 cm., raro ad 55 cm. alta) caule glanduloso-hirsuto faciebus superioribus aequalibus, radicibus tuberiferis, non-stolonifera. Folia angusta elliptica vel linearia vel oblanceolata 1—5 mm. lata 15—40 mm. longa. Antherarum appendicula 0.25 mm. longa.

Plant usually low (ca. 20 cm., rarely to 55 cm.), rigid, often bushy, tuberiferous, non-stoloniferous, glandular-hirsute. Primary axis subligneous and terete below with a thin, longitudinally flaking, cinnamon or tan bark, above four-angled, narrowly four-winged, and glandular-hairy, the faces of the stem subequal. Leaves narrowly elliptic, oblanceolate, or linear, 1.5-4.0 cm. long, 1.0-5.0 mm. broad, sessile, three-nerved with the lateral nerves often

faint and extending little more than half the length of the blade or, on narrower leaves, absent. Upper and lower surfaces of the leaves sparsely to copiously glandular-hirsute, the margins with distant, low, ascending denticles, these produced into ascending, glandular hairs. Leaves with bases acute to cuneate; leaf apex acute, usually tipped by a glandular hair. Inflorescence a densely to sparsely flowered cyme. Mature hypanthium (4.0-) 5.0-7.0 (8.0) mm. long, 3.5-5.0 mm. broad, the neck shorter than the globose body, greenish-maroon, with a scattering of glandular hairs. Calyx lobes narrowly triangular, 1.5-2.0 mm. long, spreading to ascending. Petals broadly obovate or suborbicular, 11.0-12.0 mm. long, 7.0-9.0 mm. broad, deep lavender-rose, smooth above, glandular-hairy beneath, at least in the bud. Anthers 4.0-5.0 mm. long, appendage 0.25 mm. long. Capsules subglobose or broadly ovoid, 4.0-5.0 mm. long, 3.5-4.5 mm. wide, with short, glandular hairs at the summit around the style base. Seeds cochleate, 0.7-0.75 mm. long 0.5-0.55 mm. broad, 0.3-0.35 mm. thick with 3 to 5 prominent, broad, symmetrical or vermiculate longitudinal ridges or contiguous domelike tubercles in lines, these most prominent on the crest. Chromosomes: N equals 11.

Sandy shores of limesink lakes and interdune swales along the seacoast, northwestern Florida.

Type: FLORIDA. BAY CO.: shores of Merial Lake, along Fla. Rt. 77, w.n.w. Vicksburg, *R. K. Godfrey* and *R. D. Houk 61554*. Holotype at FSU.

Remarks: There is some overlap of characteristics between *R. salicifolia* and two other tuberiferous *Rhexia*, *R. cubensis* and *R. virginica*. It resembles the former in the glandular character of its indument, in its narrow leaves, and in habit. On the other hand it suggests *R. virginica* in size and shape of hypanthium as well as in having the faces of its stems approximately equal. Comparative distinguishing features are given in tabular form below:

	R. virginica (21 localities)	*R. salicifolia* (4 localities)	*R. cubensis* (36 localities)
Stem:	4.2-11.0 dm. long, alate, faces equal; trichomes sparse, gland-tipped.	2.0-5.5 dm. long, narrowly alate, faces equal; trichomes copious, gland-tipped.	3.0-6.0 dm. long, not alate, the faces unequal; trichomes gland-tipped.
Leaves:	lanceolate or lance-ovate, (3.0-) 5.0-7.0 cm. long, (0.7-) 1.0-2.2 cm. broad, usually ascending, margin conspicuously serrate; trichomes non-glandular.	narrowly elliptic, linear or linear-oblanceolate, 1.5-4.0 cm. long, 0.1-0.5 cm. broad, often spreading, margin denticulate or entire; trichomes gland-tipped, not confined to margin and veins.	narrowly elliptic, linear, or linear-oblanceolate, 1.9-5.0 cm. long, 0.1-0.5 cm. broad, often spreading, the margin serrate; trichomes not gland-tipped, confined except in very broadest leaves to margin and midrib.
Branches:	Usually sparse, mainly from upper nodes.	Frequent, often from most of the nodes of the primary axis.	Frequent, often from most of the nodes of the primary axis.

Hypanthium:	6.0-7.0 mm. long, the neck shorter than the body; smooth to very sparingly glandular-hairy.	5.0-7.0 mm. long, the neck shorter than the body; sparsely to copiously glandular-hairy.	10.0-15.0 mm. long, the neck as long as or longer than the body; glandular-hairy.
Petals:	1.0-1.5 (-1.8) cm. long, deep lavender rose.	1.1-1.2 cm. long, lavender-rose.	1.7-2.0 cm. long, pale to deep lavender or rose.
Anthers:	5.0-6.0 mm. long, appendage ca. 0.5 mm. long.	4.0-5.0 mm. long, appendage ca. 0.25 mm. long.	8.0-11.0 mm. long, appendage 1.0-3.0 mm. long.
Seeds:	0.5-0.7 mm. long, 0.4-0.5 mm. broad, 0.25-0.3 mm. thick; tubercles dome like, in lines or irregularly formed, or surface papillate.	ca. 0.5 mm. long, 0.4-0.5 mm. broad, 0.3 mm. thick, coarsely tuberculate or with the broad narrow tubercles contiguous to form ridges.	0.6-0.7 mm. long, 0.5-0.6 mm. broad, 0.25-0.30 mm. thick, the tubercles contiguous or usually joined to form several longitudinal, narrow prominent ridges.

The above measures are from population samples ranging from 10 to 50 individuals per population.

The only other species of *Rhexia* which we have observed in association with *R. salicifolia* are *R. mariana* and *R. cubensis*. In the type locality, the flowers of *R. mariana* are uniformly white and the plants occupy higher ground than does *R. salicifolia*. In the area of Dog Lake (Dog Lake Recreational Area, s. of Tallahassee in Apalachicola National Forest, *R. Kral & R. K. Godfrey 15584*), *R. salicifolia* and *R. mariana* var. *mariana* grow in a mixed population along the shore of the lake; here the flowers of *R. mariana* are pinkish. A sample of 35 specimens all of which at first appeared to be *R. salicifolia* was taken from this locality and a seed mount made of each specimen. Four of the seed mounts showed the more finely tuberculate surface character of seed of *R. mariana* and these seed were intermediate in size between the two species. The specimens from which these four samples came were re-examined and these showed intermediate character of habit, foliage, and hypanthium. It was also evident that the capsules of the morphological intermediates had very few perfect seeds, while those of the putative parents from the same area were, on checking, filled with seed. Therefore we are of the opinion that some hybridization between *R. mariana* and *R. salicifolia* is presently occurring. In two localities near the coast of the Florida panhandle (Bay Co.: *Kral 17740*; Walton Co.: *Kral 17745*) populations of *R. cubensis* are mixed with *R. salicifolia* but though thousands of individuals of both species were present at the time of collection no evidence of hybrids was seen.

Dr. Godfrey, to whom we owe the first known collections of this species, sent material of *R. salicifolia* to Dr. James, who was of the opinion that this taxon could perhaps have been of hybrid origin between *R. cubensis* and *R. virginica*. Certainly, as the chart shows, there are several resemblances to both species. However, we have not yet found populations of *R. virginica* cohabiting the areas in which *R. salicifolia* occurs nor have we yet found

hybrids between *R. cubensis* and *R. virginica* in those few cases of mixed populations of the two; neither have such hybrids been synthesized as yet.

5. RHEXIA PARVIFLORA Chapm., Fl. ed. 3. 156. 1897. (Fig. 5, p. 424; map, p. 438.)

Low, sparingly to copiously branched, perennials from a system of short, stoloniferous rhizomes. Stems up to 4 dm. tall, the lower part somewhat woody, pale brown, usually 4-angled, at mid-stem definitely angled (sometimes with low wings as well) and the stem faces subequal, sparingly hairy or smooth save for the nodes. The larger leaves from broadly ovate to elliptic, to 3 cm. long, petiolate, the petioles up to 0.5 cm. long, sparsely, usually appressed, pubescent, the apex and base acute, the margin serrulate, the ascending teeth hair-tipped. Basal leaves usually broadest, these sometimes suborbicular, thence grading gradually into narrower but longer blades, thence gradually into bracteal leaves. Inflorescence a regularly branched, sparsely flowered, cyme. Bracts of the inflorescence similar in shape to the stem leaves, imparting to it a "leafy" look. Petals asymmetrical, suborbicular to broadly obovate, to 1.3 cm. long but usually closer to 1 cm. long, white (very rarely pale lavender), the mid-vein excurrent as a hair, the surfaces smooth. Anthers 3.0-3.5 mm. long, linear-oblong, very slightly curvate, on filaments usually shorter. Mature hypanthium 5-7 mm. long, the body subglobose, smooth, the neck short-cylindrical, shorter than the body, and with a few hairs toward the orifice. Sepal lobes ca. 2 mm. long, triangular-acuminate. Capsule smooth, subglobose. Seeds ca. 0.6 mm. long, cochleate, crested with irregular, but roughly concentric, interrupted lines of laterally flattened, dome-shaped processes, these in turn vertically grooved. Chromosomes: N equals 11.

Sunny areas or in semi-shade, on wet sands or sandy peats of cypress pondbanks, titi swamps, and Hypericum ponds, Franklin Co., Florida (quite possibly in Liberty County as well).

Type: Apalachicola, Franklin Co., Florida, *A. W. Chapman*, 1896. At MO.

Remarks: This is perhaps the rarest of the Rhexias, another of the many surprises which Dr. Chapman turned up from the swamp country around Apalachicola. It is indeed similar to white-flowered *R. mariana* var. *mariana*, and populations of that entity are always nearby. Yet is is a different looking plant, with its characteristically shorter rhizomes, smoother stems, broader leaves (*R. mariana* var. *mariana* in this area is narrow-leaved), shorter, broader petals and shorter anthers. Strangely enough, its epidermal character is closest of all to that of *R. aristosa*, another rare but much different species.

Three rather large samples of *R. parviflora* (*Kral & Godfrey 15050*, *Kral 15702*, and *Kral 17784*), gotten from Franklin County, Florida recently have been distributed. One will note from the label information that the habitat these plants are in is quite different than that of *R. mariana* var. *mariana*. The latter is very weedy and abounds on much drier substrates. In fact, the access road to the area in which *R. parviflora* occurs has abundant patches

of *R. mariana* on its sandy shoulders, while *R. parviflora* appears to stay on the wetter soils through which the road passes. Winter leaves of both species both may be broad, but while the leaves of north Florida populations of *R. mariana* tend to lengthen and narrow, sometimes even become filiform, the summer leaves of *R. parviflora* show no such extreme. Therefore, if the difference distinguishing *R. parviflora* from white-flowered extremes of *R. mariana* var. *mariana* are few, they appear to be consistent. It is remarkable that this little plant, with a wealth of what looks to be similar habitat in north Florida and Georgia, is so restricted in known range. The niche it occupies must be extremely refined.

6. RHEXIA ARISTOSA Britton, Bull. Torrey Club 17: 14, pl. 99. 1890. (Fig. 6, p. 425; map, p. 438.)

Stiff, sparingly or profusely branched, perennials from a spongy, usually tuberiferous base. Shoots 4-7 dm. long, thickened, sometimes spongy and flaky barked and subterete toward the base, becoming tan or green and subequally four-sided at midstem, the stem angles darker green than the faces, and sometimes produced into low wings. Surface of stem glabrous save for a few long, flaring yellowish trichomes at the leafy nodes. Leaves predominantly lanceolate, ascending, the longest 2-3 cm. long, 3-5 mm. broad, pale green, the lower surfaces smooth to sparingly appressed-hairy and prominently triple-veined, the upper surfaces similarly smooth or hairy, the apex acute to obtuse, mucronate, the margin with low but regular, ascending, aristate teeth. Leaves gradually becoming longer upward into mid-stem (those of the often numerous lateral shoots noticeably smaller), and passing gradually into bracteal leaves which often closely invest the flowers, later fruit. Inflorescence most commonly a broadly paniculate cyme, branching so that the hypanthia appear to develop on the adaxial side of the major branches. Petals broadly, but asymmetrically oblong-obovate, up to 2.2 cm. long, dull lavender (similar and size and colour to *R. nashii*), the eccentric midvein excurrent as a long, tapering hair; outer surface of petals appressed-hairy, particularly toward the margins. Anthers at anthesis linear-lanceolate, curvate, 5-6 mm. long, on filaments to 8 mm. long. Mature hypanthia 7-10 mm. long on stout terete pedicels to 3 mm. long; base ovoid, tapering into a cylindrical neck of about the same length, this flaring above into the rim; sepal lobes narrowly triangular, horizontally spreading, aristate; hypanthial hairs usually restricted to hypanthial neck, rim, and lobes, stiff but slender-tapering, yellowish, the rim hairs tending also to flare horizontally. Capsule oblong-ovoid, smooth. Seeds cochleate, ca. 0.7 mm. long, irregularly but concentrically ridged with a few isolated domes or papillae. Chromosomes: N equals 11.

Peats and sandy peats of pine flatwoods bogs, cypress domes and savanna ditches, very local, New Jersey, the Carolinas, Georgia and southwestward into southeastern Alabama, always in the Coastal Plain.

Type: May's Landing, Egg Harbor City, Atlantic Co., N.J., *Kilmer & Gifford*, Aug. 1888. At NY.

Remarks: This rare plant is one of the most distinctive in the genus, with its bushy, tuberiferous, habit, its large, pale-lavender flowers, its stiffly spreading, aristate sepal lobes, and its flaring, yellowish hypanthial hairs. Its general habit and its angular stems have some overlap in character with forms of *R. virginica*, but in character of its upper epidermis (see plate) it is surprisingly like the Florida endemic *R. parviflora*.

7. RHEXIA VIRGINICA L., Sp. Pl. 346. 1753. (Fig. 7, p. 426; map, p. 438.)

R. septemnervia Walt., Fl. Carol. 130. 1788.

R. stricta Pursh, Fl. A. Sept. 1: 258. 1814. non Bonpl. Melast. II. Rhex. 19, pl. 8.

R. purshii Spreng., Syst. 5: 590 (index). 1828.

R. virginica L. var. *purshii* (Spreng.) James, Brittonia 8: 227. 1956.

Rigid, simple or sparingly branched, perennials from spongy-thickened or tuberiferous rootstocks. Shoots solitary or a few, to 1 meter tall, subterete spongy-thickened, and subterete toward the base, sometimes with a thin, reddish-brown, exfoliating bark, becoming 4-sided and wing-angled in the mid and upper portions, glandular-hairy to almost smooth save for a few hairs at the nodes. Leaves ascending, ovate to elliptic but commonly lanceolate, 3-5 (-7) cm. long, acute to acuminate, serrulate with the ascending tips of the teeth often hair-tipped, the base rounded to acute, sessile or short-petiolate. Lowermost leaves gradually shortening to the inflorescence, thence more or less abruptly reduced to much smaller bracteal leaves or scales. Inflorescence few-to-many-flowered, open or contracted, regular cyme, which has a naked appearance because of the reduced bracts. Petals asymmetrical oblong to obovate, 1.5-2.0 cm. long, lavender-rose, the midrib exserted as a glandular hair, some hairs usually also present on the petal backs. Anthers linear-curvate, ca. 5 mm. long on filaments of the same length or slightly longer. Mature hypanthium 7-10 mm. long, smooth or glandular-hairy, the body globose, gradually or abruptly contracting into a narrow neck shorter than the body, thence flaring into narrowly triangular acute to acuminate calyx lobes 3-4 mm. long. Seeds ca. 0.7 mm. long, cochleate, the surface ranging from low-muricate to papillate or tuberculate, the processes contiguous, in concentric lines and most prominent toward the crest. Chromosomes: N equals 11, 22.

Wet sands and peats of pondshores, ditches, bogs, pine flatwoods and savannas southeastern Canada south throughout almost all of the U.S.A. east of the Mississippi and westward into Texas, Missouri and Iowa.

Type: Virginia, *Clayton 227*. At BM.

Remarks: This wide-ranging species has been treated by James as comprising two varieties. The criteria employed were degree of pubescence of stem, hypanthium, bracts and petals together with lengths of calyx lobes in relation to hypanthial neck. There is some clinal change southward in the U.S.A. toward smoother plants having relatively longer calyx lobes, but both sorts of plants are found as far south as northern Florida and, as James

himself concedes, it is often difficult to know where to draw the line between the two varieties.

R. virginica often grows in close proximity to *R. mariana*, but as a rule is on moister substrata. Generally, it develops from tubers, but often produces rhizomes as well. On mucky soils it often perennates from a very stout, spongy caudex, rather than from tubers.

It is difficult to distinguish extremes of this species from *R. mariana* var. *ventricosa* or *R. mariana* var. *interior*. However, both varieties of *R. mariana* are exclusively rhizomatous, have a tendency toward longer, hairier hypanthia, and lack the broad wing-angles of the stem.

Hybrids between *R. virginica* and *R. mariana* var. *mariana* are frequently collected.

8. RHEXIA MARIANA L. var. MARIANA, Sp. Pl. 346. 1753. (Fig. 8a, p. 427; 8b, p. 428; map, p. 439.)

R. lanceolata Walt., Fl. Carol. 129. 1788.

R. mariana L. var. *rubella* Michx., Fl. Bor.-Am. 1: 221. 1803.

R. angustifolia Nutt., Gen. 1: 244. 1818. Ell., Sk. Bot. S.C. & Ga. 1: 438. 1821.

R. mariana L. var. *lanceolata* (Walt.) Wood & McCarthy, Journ. Elisha Mitchell Soc. 3: 97. 1866.

R. delicatula Small, Fl. SE. U.S. 824. 1335. 1903.

R. filiformis Small, Bull. Torrey Club 25: 468. 1898.

Hirsute, weedy perennials, forming extensive clones from shallowly set, elongate, stoloniferous rhizomes. Shoots 2-10 dm. tall, terete, the bases sometimes subligneous and with a reddish-brown, slightly exfoliating, thin bark, greenish or yellowish-green and spreading-hairy in the leafy portion, simple or freely branching from the mid-stem upwards. Leaves from linear-filiform to lanceolate, elliptic or even narrowly ovate, the longer ones mostly 2-4 cm. long, sessile or short-petiolate, sparsely to copiously appressed-hirsute, dark to pale yellow-green, the apex acute to acuminate, the margins serrulate, the teeth apiculate, or hair-tipped, the base acute to attenuate. Basal leaves usually broadest and petiolate, becoming longer and of a narrower type toward the midstem, thence gradually shortening to the base of the main inflorescence, thence abruptly replaced by small, linear, elliptic-linear, or ovate bracts. Inflorescence a few to many-flowered, open or congested cyme, the fruiting hypanthia often arranged in secund fashion toward the inside of the main branches. Petals asymmetrical, broadly cuneate, oblong or obovate, 12-15 mm. long, white to dull lavender, rarely lavender-rose, the apices often noticeably truncate-oblique, this interrupted only by the aristate excurrent mid-vein, the surfaces of the blade characteristically smooth. Anthers at anthesis linear-lanceolate, curvate, 5-8 mm. long on filaments of about the same length. Mature hypanthia 6-10 mm. long on pedicels 1-3 mm. long; hypanthial body ovoid to subglobose, more or less evenly tapering into a cylindrical or slightly upwardly expanding neck which is at least as long as the body; sepal lobes narrowly triangular, acute or acuminate, 2-3 mm.

long. Hypanthial hairs spreading, frequent to sparse, rarely absent (this most often the case in peninsular Florida forms). Capsule smooth, globose. Seed cochleate, ca. 0.7 mm. long, the surface longitudinally ridged with contiguous tubercles, papillae or laterally flattened domes, the most prominent ridges along the crest, or rarely almost smooth. Chromosomes: N equals 11, 22.

Sands, gravels, or sandy peats of pine flatwoods, bog margins, ditches, disturbed grounds, and particularly highway and railroad embankments, eastern Massachusetts south to the tip of Florida, west in the interior into the Central Lowlands and Interior Highlands, west in the Coastal Plain to Central Texas.

Type: Pluk. Almag. Bot. Mant. pl. 428. f. 1. 1700 (In part, in sensu Cogniaux, non. Walter, according to C. James, 1956).

The most difficult part of a study of *Rhexia* centers with this species. It is undoubtedly the most abundant, wide-ranging, and weediest species; it comes into contact with every other entity of *Rhexia* and hybridises with many. It often takes on several of the characteristics of other species in areas where that other species is the most abundant, and yet retains even in such cases a sufficient reservoir of individuality to mark it as *R. mariana.*

James' (l.c.) treatment stresses the existence of a white or pale-lavender flowered, narrow-leaved, small hypanthiumed variety (*R. mariana* L. var. *exalbida* Michx), and this might be held tenable on the basis of the floras of the Atlantic and eastern Gulf coastal plains. However, after examining specimens from this region in a broader context of Texas, Louisiana and southern Mississippi populations, as well as those populations of *R. mariana* from peninsular Florida, we are hard put to come to the same conclusion. As James himself states "all of the characters studied which have been used to distinguish it (*R. mariana* var. *exalbida*) from var. *mariana* are quantitative and intergradation does exists to some degree." While composite populations having narrow leaves, smooth hypanthia, smoother seed, and pale flowers are not rare, none of these features appear to vary consistently on a clinal basis. For example, as one travels west in the Gulf states, white-flowered *Rhexia mariana* with longer, hairier hypanthia and broader leaves are quite frequent; as one travels south into the peninsula of Florida, the flowers of this species tend to be lavender-rose or deep lavender (similar in colour to *R. cubensis*) while the leaves remain linear and the hypanthia remain smoothish. To the north, in the Atlantic coastal plain, all of the characteristics may vary independently. Therefore, we have inclined toward an even more conservative treatment than that of James, and in a search for some geographical basis for variation in the whole complex have abandoned altogether the var. "exalbida" while reducing the status of two more related entities, *R. interior* Pennell and *R. ventricosa* Fern. & Grisc. to that of varieties of *R. mariana* (see discussion under these varieties).

Plants which might be called *R. mariana* var. *exalbida* do show some constancy of chromosome complement. However if one recognizes this taxon,

then the only feature that distinguishes it from the typical variety of *R. mariana* is the chromosome number (and that does not hold true consistently). In the eastern United States, the typical *R. mariana* has a chromosome number of twenty-two (tetraploid); while, in the western portion of the range, the chromosome number is eleven (diploid). The chromosome number of *R. mariana* var. *exalbida*, if recognized, is eleven.

9. RHEXIA MARIANA L. var. **ventricosa** (Fern. & Grisc.) Kral & Bostick, comb. nov. (Fig. 9, p. 429; map, p. 440.)

R. ventricosa Fern. & Grisc., Rhodora 37: 172, pl. 346, f. 1-4. 1935.

As in *R. mariana* but rhizomes stouter, the stems tending to have subequal faces, the stem angles sharp or quite narrowly winged, the stem surfaces often smoother. Leaves larger. Flowers larger (the petals to 2.5 cm. long) of similar shape but bright lavender-rose (in contrast to contiguous populations of *R. mariana* var. *mariana* which have dull lavender petals), the backs of the petals with at least some appressed hairs (in contrast to contiguous populations of *R. mariana* var. *mariana* which have smooth petals). Hypanthia similar in shape but longer (1-1.2 cm. long), usually hirsute. Seed of similar shape and size, but with close-set papillae in concentric lines. Chromosomes: N equals 22.

Moist to wet sands, peats or sandy peats, of roadbanks, ditches, clearings in cypress-hardwood swamps and flatwoods, coastal plain, New Jersey south into South Carolina.

Type: open clay at border of woods, east of Little Creek, Princess Anne Co., Virginia, *Fernald & Long 4064*. At GH (Isotype at NY examined).

This variety, although it has more characteristics in common with *R. mariana* than with other species may be confused with *R. nashii* or with the variety *interior* of *R. mariana* (which see). However, it may be distinguished from the former by its brighter coloured flowers and hairy hypanthia (*R. nashii* flowers are dull lavender and its hypanthia are smooth) as well as by its subequal stem faces. The only striking character difference this variety was with the var. *interior* appears to be its seed, the surfaces of which have lines of papillae in contrast to the ridged surfaces of seed of the latter.

10. RHEXIA MARIANA L. var. **interior** (Pennell) Kral & Bostick, comb. nov. (Fig. 10, p. 430; map, p. 440.)

R. interior Pennell, Bull. Torrey Club 45: 480. 1918.

As in *R. mariana* but rhizomes stouter, the stems tending to have subequal faces, the stem angles sharp or narrowly winged, the stem surfaces often smoother and with hairs concentrated at or toward the nodes. Leaves larger, usually elliptical or ovate to ovate-lanceolate, the short petioles often maroon. Flowers similar to *R. mariana* in shape but sometimes larger and consistently a bright lavender-rose and the backs of the petals usually with some appressed hairs. Hypanthia as in var. *mariana* but larger (1.0-1.3 cm. long), usually hirsute. Seed ridged, particularly along the crest, the ridges

interrupted or of laterally flattened, dome-like processes. Chromosomes: N equals 22.

Moist to wet sands, sandy clays, or peats of roadbanks, ditches, swamp forest clearings, prairies, glades or flatwoods, southern portion of the Central Lowlands (Indiana, Kentucky, Tennessee) south into west-central Mississippi, thence west to the prairie border in north Texas, Oklahoma, but centering in the Interior Highlands.

Type: high prairies, Alba, Jasper Co., Missouri, *Bush 6070.* At MO. Isotype at NY examined.

The great similarity of this variety to the variety *ventricosa* is inescapable. Yet a considerable distance separates the two, at least as their ranges are now understood, and would lead one to assume either an independent origin of similar morphology (by hybridization) or a relict "pair" which at one time was contiguous. James (l.c.) has speculated that both *R. interior* and *R. ventricosa* could have originated through hybridization between *R. mariana* and *R. virginica*, yet the appearance of such hybrids (which are fairly frequent in Georgia and north Florida) is quite different. Our experience with *R. mariana* var. *interior* is that its flowering time overlaps that of *R. mariana* more closely than it does that of *R. virginica* and that intermediates between these two entities are not uncommon.

There appears to be some morphological range within the variety *interior*. Populations of northern Louisiana have larger stature, larger flowers and hypanthia than those of the Ozarks from which the type material was described. (Compare Louisiana numbers *15716*, *15744*, *15948*, *19400*, *20325*, *23275*, *23239*, *24521* with Arkansas numbers *24600*, *24603*, *24574* and Oklahoma *24607*). Yet, in that portion of northern Louisiana in which this variety is found, *R. virginica* is quite rare, certainly having none of the weedy character common to all varieties of *R. mariana* and little opportunity appears to arise for much exchange of pollen between the two.

11. RHEXIA CUBENSIS Griseb, Cat. Pl. Cub. 104. 1866. (Fig. 11, p. 431; map, p. 437.)

R. mariana L. var. *portoricensis* Cogn. Jahrb. Bot. Gart. Berlin 4: 276. 1886.

R. floridana Nash, Bull. Torrey Club 22: 150. 1895.

Profusely rhizomatous (also tuberiferous) strict or bushy perennials. Shoots 3-6 cm. long, glandular hirsute, subterete, subligneous, with thin, reddish-brown bark toward the base, upwardly greenish. Leaves predominantly linear, linear-elliptic, oblong, or narrowly spatulate, (only the midrib prominent), 2-4 cm. long, pale to deep green or with maroon tints, both surfaces with a scattering of long, glandular trichomes, the apex obtuse to short-acuminate, the margin regularly low-toothed, the teeth ascending and each terminating in a glandular hair. Leaves grading gradually upward to longest toward midstem, thence becoming gradually shorter into the inflorescence, where they abruptly shorten into narrowly elliptic or short-linear bracts. Inflorescence a few-to-several-flowered, paniculate cyme, the

hypanthia tending to develop in secund fashion on the inner side of the inflorescence branches. Petals broadly cuneate or obovate, 1.5-2.0 cm. long, spreading horizontally, bright lavender-rose or sometimes paler, almost white toward the short-clawed base, smooth or with a very few glandular hairs on the backs, the midvein exserted as a hair. Anthers at anthesis linear-lanceolate, curvate, 7-10 mm. long, on filaments of about the same length. Mature hypanthium 10-14 mm. long on pedicel 2-3 mm. long; hypanthial base ovoid or subglobose, usually tapering into a gradually expanding neck at least as long as the hypanthial body; sepal lobes narrowly triangular or oblong, usually reflexed at fruiting time, acute. Hypanthial hairs scattered, glandular, sometimes sparse or wearing away by maturity. Capsule smooth, subglobose. Seed cochleate, ca. 0.7 mm. long, concentrically and rather evenly ridged, particularly along the crest. Chromosomes: N equals 11, 22, 33.

Peats and sandy peats of pine flatwoods, ditches, margins of bogs, and hillside seepage areas, not infrequently a weed of roadsides, eastern North Carolina south to the tip of Florida, west in the Coastal Plain to southwestern Mississippi; in the West Indies, such as Cuba, Dominican Republic, Puerto Rico.

Type: damp ground near lagunas Asiento Viejo in San Julian, Cuba, *Wright*. Isotype at GH.

R. cubensis could only be confused with narrow-leaved examples of *Rhexia mariana* var. *mariana*, particularly populations of the latter which have lavender-rose petals. This situation is most encountered in peninsular Florida, where *R. mariana*, chameleon-like, takes on some "cubensis" character. However, *R. mariana* never produces tubers, its flowers in that region are consistently smaller, and its hypanthia much smaller and smoother. Seed characteristics do not always suffice to distinguish these two entities.

R. cubensis grows closer to the present coast than do most other Rhexias (with the possible exception of *R. mariana*, *R. salicifolia*, *R. virginica*), and is probably the commonest species of the slash pine flatwoods of peninsular Florida. While breeding studies at this point do not show that F-1 hybrids between *R. cubensis* and *R. mariana* or *R. nashii* produce viable seed it is still possible that such a phenomenon may, on occasion, occur.

12. RHEXIA NASHII Small, Fl. SE. U.S. 824. 1335. 1903. (Fig. 12, p. 432; map, p. 437.)

R. mariana L. var. *purpurea* Michx., Fl. Bor.-Am. 1: 221. 1803.

Hirsute perennials, forming extensive clones from shallowly set, elongate, stoloniferous, sometimes tuberiferous, rhizomes. Shoots (2-) 3-10 (-15) dm. tall, the lower portion brownish or reddish-brown, subligneous and often with exfoliating bark, becoming hirsute, greenish or yellowish-green or reddish-green by mid-stem. Leaves commonly of an ovate, lance-ovate, elliptic or lanceolate shape, 3-7 cm. long, yellow-green, both surfaces hirsute, the apex acute, the margins finely to rather coarsely serrate, the teeth drawn out into hairlike tips and often with hairs on their margins; leaf bases acute,

often short-petiolate. Leaves gradually shortening into the inflorescence; bracts of similar shape and vesture to foliage leaves but much smaller. Inflorescence an open or contracted, symmetric cyme, the fruiting hypanthia sometimes secund on the inside of the cyme branches. Petals asymmetrically and broadly obovate or even suborbicular, 2.0-2.5 (-2.7) cm. long, usually dull lavender, the mid-vein exserted as a short hair, the backs appressed hairy. Anthers 8-11 mm. long, linear-lanceolate, on filaments of corresponding length. Mature hypanthium glabrous or glabrate, 10-15 (-20) mm. long on pedicels 2-4 mm. long; hypanthial body ovoid to subglobose, abruptly or gradually passing into the cylindrical or narrowly funnelform neck which is at least equal in length; sepal lobes narrowly triangular, acute or acuminate, 2-4 mm. long. Capsule pyriform, usually completely glabrous. Seeds about 0.7 mm. long, cochleate, the surfaces concentrically lined with contiguous, dome-shaped, sometimes laterally flattened, processes, these most noticeable on the crest of the seed. Chromosomes: N equals 22, 33.

Acid, sandy or peaty swamps and bogs, roadside ditches, and flatwoods, invariably on wetter substrates than *R. mariana*, Coastal Plain, eastern Virginia south to southern Florida and west to the Florida parishes of Louisiana.

Type: swamps, in the vicinity of Eustis, Lake Co., Florida, *Nash 863*. At NY.

R. nashii, which so often resembles a large version of *R. mariana* var. *mariana*, invariably may be distinguished from that variety by its smoother hypanthia, much larger petals, and especially by its petal hairs. This latter characteristic is particularly useful on herbarium specimens, in that the hairs of *R. nashii* petals are best developed on that portion of the petal backs exposed on the bud.

A greater problem is in distinguishing *R. nashii* from *R. mariana* var. *ventricosa*, which itself has hairy petals and large hypanthia, together with some similarities in habitat, habit and leaf. However the latter may be distinguished by its more rose-tinted petals, the hair of its hypanthia, and its subequal stem faces. So far as we know the ranges of *R. nashii* and *R. mariana* var. *interior* do not overlap or a similar problem of identification would exist for these collections.

R. nashii and *R. mariana* frequently hybridise. Such have been reported by James, and we have made similar observations (*Kral 15678-15679, 19111-19112*). Occasional intermediate morphologies between it and *R. cubensis* are to be found in peninsular Florida. In southern Alabama, Mississippi and in northern Florida it frequently hybridises with *R. virginica*, a fact confirmed by breeding studies.

13. RHEXIA ALIFANUS Walt., Fl. Carol. 130. 1788. (Fig. 13, p. 433; map, p. 437.)

R. glabella Michx., Fl. Bor.-Am. 1: 222. 1803.

R. glabella Michx. var. *alifanus* (Walt.) Pursh, Fl. Am. Sept. 1: 258. 1814.

Tall, 6.5-11.5 (-20) cm., sparingly-branched, perennials from a stout, pithy, deepset caudex. Shoots glabrous, usually unbranched below the inflores-

cence, the lowest portion terete, reddish-brown, occasionally with a thin, exfoliating bark; upper portion greenish, each internode somewhat flattened in a plane parallel to that of the subtending leaf pair, and longitudinally striate, the narrower, paler green bands aligned with leaf midribs. Leaves predominantly lance-ovate to elliptic or lanceolate, at mid-stem 3.5-7.5 cm. long, 7-10 (10.5) mm. broad, smooth, bluish or yellowish-green, evidently triplenerved, subsessile, the apex acute or short-acuminate, the margin entire or remotely low-toothed apically the base cuneate. Leaves gradually becoming longer toward mid-stem, then gradually reduced into the inflorescence, there abruptly giving way to small (2-3 mm.) ovate, glandular-hairy, caducous, bracts. Inflorescence a regular, oblong or spreading, paniculate cyme. Petals broadly oblong to suborbicular, 2.0-2.5 cm. long, lavender-rose, the principal veins asymmetrical, palmate, purple, the midvein exserted as a short, fine mucro, the inner surface smooth, the outer surface with some hairs on the small-area side of the midvein beneath. Anthers at anthesis yellow, linear-lanceolate, curvate, 7-8 mm. long, short-appendaged, on filaments 6-8 mm. long. Mature hypanthia usually glandular-hairy, 7.5-10.0 mm. long, on stout, terete, pedicels 3-4 mm. long and markedly broader than the subtending inflorescence branches; hypanthial base subglobose to broadly ovoid, longer than the abruptly constricted neck; hypanthial neck flaring abruptly into a flange-like orifice nearly as broad as the hypanthial base. Sepal lobes oblong or narrowly triangular, acute or blunt, usually smooth. Capsule pyriform, smooth or with a few scattered hairs apically. Seeds oblong to wedge-shaped, 1-2 mm. long, smoothish. Chromosomes: N equals 11.

Sandy peat of pine flatwoods, bogs, sevannas, Coastal Plain, eastern North Carolina south into northern peninsular Florida, thence west into eastern Texas.

Type: cutover, low, wet pineland 8 mi. w. Pineville, Berkeley Co., S.C. *James 675*. (This a neotype deposited at GH).

This *Rhexia*, with its smooth, wand-like stems, smoothish cleancut leaves, large showy flowers and conspicuously glandular-hairy hypanthia is one of the most clearly marked species in the genus and may actually have closer affinities with some tropical-American genus. Its seed, sometimes fully twice the size of that of other *Rhexia*, differs also in its unique, usually somewhat triangular, shape.

The distribution of *R. alifanus* in Florida is rather interesting, closely paralleling that of the yellow flowered *R. lutea*, in that its southern limits there are in the northern part of the peninsula (Volusia Co.). It is most abundant in and about the *Stokesia-Sarracenia* bogs of northwest Florida, southern Alabama, and southern Mississippi.

RHEXIA HYBRIDS

As James has observed, it would appear that no natural hybridization involving *R. nuttallii*, *R. petiolata*, *R. lutea*, *R. parviflora* or *R. alifanus* occurs. However, artificial hybrids between *R. nuttallii* and *R. petiolata* have

been gotten which have produced full seed. James got viable seeds from crosses he made between *R. virginica* and *R. nashii*, and *R. mariana* and *R. nashii*; he also has observed hybrids between *R. aristosa* and *R. virginica*, *R. virginica* and *R. mariana*. All these have been observed in the field or in the greenhouse during this particular study. Some comment about this follows.

Naturally occuring hybrids. Hybrid swarms involving *R. mariana* var. *mariana* and *R. nashii* are not uncommon; samples from such swarms (i.e. *Kral 15678-15679*, *Kral 19111-19112*) show a gradual transition from tall plants with large, smooth hypanthia and broadly lanceolate or elliptic leaves to lower plants with much smaller hypanthia and lineal leaves; flowers in these samples range gradually from large, lavender petals to much smaller and paler corollas; seed characters are likewise variable. Hybrid swarms involving *R. mariana* var. *mariana* and *R. virginica* are also fairly frequent (i.e. *Kral 15555*, *15685*, *19307*, *19325*, *28634*, *28637*, *28638*, *28640*); the F-1 is a plant of intermediate height and stockiness, with angled but not winged stems, with narrowly lanceolate to almost lineal leaves, hypanthia of about the size and shape of *R. mariana* but with very few full seed in the capsules, and only a scattering of ripe fruit, most having shrivelled and fallen from the plants. However, some backcrosses do appear or at least there are morphologies in such populations that would be difficult to explain otherwise. In these latter cases a greater proportion of capsules remain on the plant and a larger number of full seed is found, as would be expected. One case of hybridization between *R. mariana* var. *mariana* and the new species, *R. salicifolia* is here reported; however this must be of rare occurrence, for none have been reported from any other of the several localities where both are found. In northwest Florida, southern Alabama, and in southern Mississippi samples have been collected from several naturally occurring hybrids of *R. nashii* and *R. virginica*. These are recognized by their rhizomatous habit (a *nashii* character), greater amount of maroon pigmentation of stem and foliage (a *virginica* character), four angled, but not winged, stems, their sparsely hairy hypanthia which are longer than *R. virginica* but shorter than *R. nashii*, their bright lavender-rose petals which are larger than those of *R. virginica* but smaller than those of *R. nashii*, and their intermediate seed character. Examples at VDB are *Demaree 32982*, *Kral 17449*, *Kral 15649*, *Kral 22052*, *Kral 22046*, *Kral 25859*, *Kral 25847*, *Kral 29676*. While experimental hybrids between *R. mariana* and *R. cubensis* do not themselves form viable seed, it is to be suspected that this must sometimes happen in nature. There is hardly any other explanation for the fact that in peninsular Florida populations of *R. mariana* take on many "cubensis" characteristics such as (a.) more glandular pubescence (b.) more maroon pigmentation (c.) "cubensis" type leaves and leaf arrangement (d.) the deep and bright lavender-rose petal colour. Whole populations of *R. mariana* var. *mariana* may have the characteristics mentioned and yet examples of actual F-l's between these and *R. cubensis* which cohabits the areas are not

found. Perhaps the paradox could be explained in terms of very occasional seed being formed by very infrequent F-l's, this germinating and establishing populations vegetatively and subsequently backcrossing to form what comprise the common *R. mariana* of southern Florida.

Experimental hybridization. Living transplants were maintained at the North Carolina Botanical Garden at Chapel Hill, North Carolina. Fine-mesh nylon stockings were used as bags to prevent normal insect pollination. Stamens from the pollen parent were removed and the pollen was teased out of the anther with a needle. The pollen was transfered to receptive stigmas of newly opened, emasculated flowers of bagged plants. At least three duplicates were made of each cross and reciprocal crosses were made in each case. Seed formed, if any, was collected as the capsules matured and sowed onto a 1:1 mixture of sand and peat in plastic pots. The pots were placed in trays, watered from beneath, and placed in a cold room for a month. The trays were then removed to a greenhouse and watered from beneath once a week.

Apparently, the chief isolating mechanism(s) operating within most of the taxa of the genus is an incompatibility factor or factors. Stebbins (1966) has classified isolating mechanisms into two large categories: prezygotic, in which fertilization and zygote formation are prevented in various ways and postzygotic, in which fertilization takes place and hybrid zygotes are formed, but these are inviable or give rise to weak or sterile hybrids.

In artificial crosses within *Rhexia*, three types of results were obtained (Fig. 14):

1. Seeds were not formed.
2. Seeds were formed and would not germinate.
3. Seeds were formed and would germinate.

In those crosses in which no seeds were formed within the receptive flower, it is presumed that the isolating mechanism involved is prezygotic, since the gametes probably never fused. The actual mechanism here could be a stigma- or style-pollen incompatibility. It must also be recognized that there is a possibility that the isolating mechanism involved in these crosses occurs at a very early postzygotic stage. This might account for the failure of seed formation.

In those crosses in which seeds were formed but would not germinate, the isolating mechanism must be postzygotic, since these seeds, when dissected, were found to contain embryos but no endosperm.

In those crosses in which seeds were formed and would germinate, the seeds were found to contain both embryos and endosperm. However, the progeny of these crosses have all died since the crosses were made. This could be the result of poor cultural conditions or of another postzygotic mechanism.

The only species which formed viable seeds when self-pollinated (pollen and stigma of same flower and pollen and stigma of different flower but same plant) were *Rhexia petiolata* and *R. lutea*. Whether or not self-pollina-

tion (and self-fertilization) occurs regularly in nature remains in doubt. From breeding studies, it has been learned that plants of these two species will also form viable seeds when outbred. All of the other taxa are obligate outbreeders.

When an artificial cross "took," the plants involved were invariably of the same ploidy level. When no viable seeds were formed, the isolating mechanism was postzygotic (inviable seeds formed) if the ploidy levels were the same, or was presumably prezygotic (no seeds formed) if the ploidy levels were different. Crosses at the hexaploid level never resulted in the formation of viable seeds.

PAPER CHROMATOGRAPHY

Extracts of leaves from the third node below the base of the inflorescence of herbarium specimens and of petals of the same specimens were made with 0.5% hydrochloric acid in methanol. Two-dimensional descending paper chromatograms of all taxa were prepared with the first-dimension solvent of 3 tertiary butanol: 1 glacial acetic acid: 1 water. The second-dimension solvent was 15% acetic acid. The chromatograms were dried and viewed against ultraviolet light in ammonia vapor. An effort was made to sample each taxon from representative localities throughout its range. Compounds appearing as chromatogram spots were not identified but the colors and spot patterns were used as taxonomic devices.

Very little intraspecific variation in chromatographic patterns was observed: hence it was possible to characterize each taxon or ploidy level with a "type chromatogram" (Fig. 15-50). Chromatograms of leaves and petals gave approximately equivalent results, although petal chromatograms were more useful in separating one taxon from another. Spots of the two types of chromatograms were not the same but, in most cases, the chromatographic affinities of the groups were expressed in the same manner. Table II presents the results of a survey of the number of distinctive spots for each taxon.

One of the most interesting chromatographic patterns obtained was that of *Rhexia alifanus*. In both leaf and petal chromatograms, this species had very few spots in common with the other taxa of the genus.

The petal chromatograms of the yellow-petaled *R. lutea* show little affinity to those of other species. The leaf chromatograms have no distinctive spots but are unique in that only two spots are present.

Although Series A (Small's Ellipticae) shows little chromatographic affinity to Series B (Small's Lineares), its members show even less affinity to one another. *Rhexia nuttallii* leaf chromatograms have about 40% of their spots in common with members of Series B and about 27% of *R. nuttallii* spots are shared with the other two species of Series A.

Chromatography has shed some light on the question, originally raised by James (1956), of the possible intermediacy of *Rhexia parviflora* to Series A and Series B. *Rhexia parviflora* shares 62% of its petal chromatogram spots with *R. petiolata* of Series A and this is considerably higher than the percent

TABLE II

DISTINCTIVE CHROMATOGRAPHIC SPOTS IN *RHEXIA*

Taxon	*Leaf Chromatograms*		*Petal Chromatograms*	
	No. of Spots	*Number Distinctive*	*No. of Spots*	*Number Distinctive*
R. petiolata	14	3	6	0
R. nuttallii	7	1	8	1
R. lutea	2	0	5	5
R. salicifolia	9	0	3	0
R. parviflora	5	0	7	0
R. aristosa	7	0	4	0
R. virginica, n=11	6	0	6	0
R. virginica, n=22	8	1	9	1
R. mariana var. *interior*	7	0	11	0
R. mariana var. *ventricosa*	7	0	12	0
R. mariana, n=11	6	0	11	0
R. mariana, n=22	8	0	9	0
R. cubensis, n=11	6	0	5	0
R. cubensis, n=22	7	0	6	0
R. cubensis, n=33	7	0	7	0
R. nashii, n=22	8	0	7	0
R. nashii, n=33	9	0	8	0
R. alifanus	21	13	9	3

shared with at least half of the other members of Series B—its morphologically closest relatives.

Rhexia interior and *R. ventricosa* have been said to be of possible hybrid origin by James, who indicated that *R. mariana* and *R. virginica* could be possible parental species. Chromatographic studies seem to support the hypothesis that *Rhexia interior* and *R. ventricosa* may be rather closely related to *R. mariana*. The tetraploid forms of *R. mariana* and *R. virginica* (n = 22) have exactly the same number of spots in common with *R. interior* and *R. ventricosa*, both of which are also tetraploid taxa. *Rhexia interior* and *R. ventricosa* show more chromatographic affinity to each other when leaf chromatograms are compared (100% of spots in common) than when petal chromatograms are compared (64% of spots in common); but are definitely closely related, both chromatographically and morphologically. Indeed, other than by the use of James' seed characteristics, the only way that many students are able to separate the two taxa is by their distributions. All of the above data lend weight to our opinion that *R. interior* and *R. ventricosa* should receive no more than varietal status within *Rhexia mariana*.

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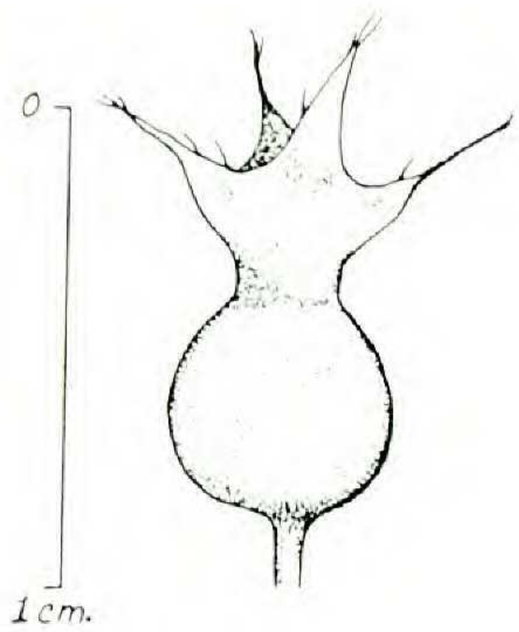
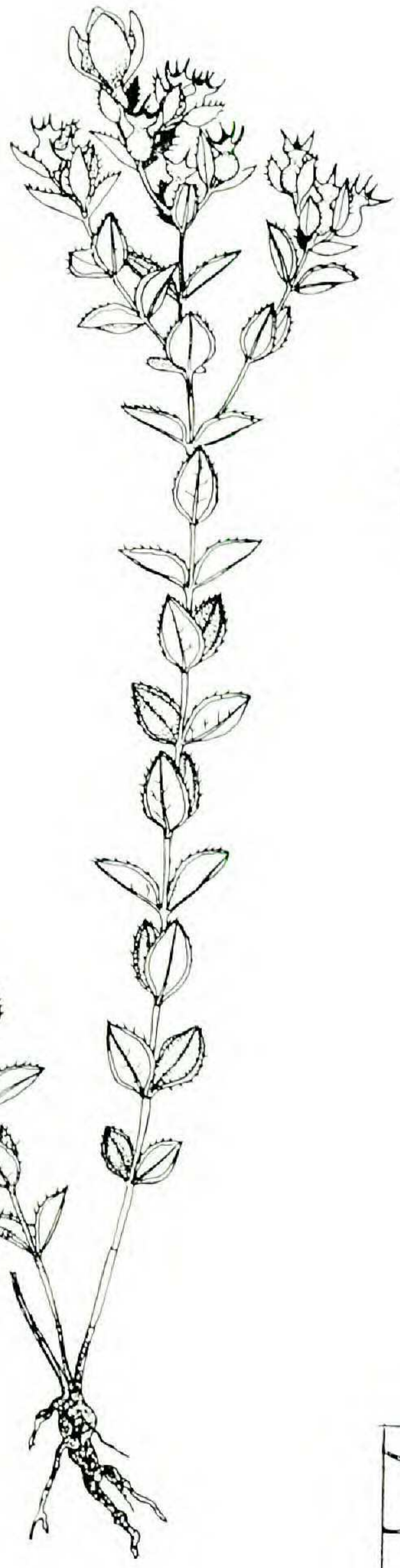
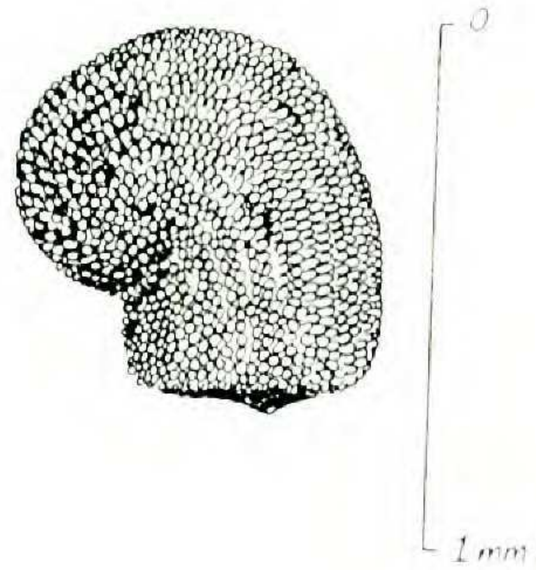
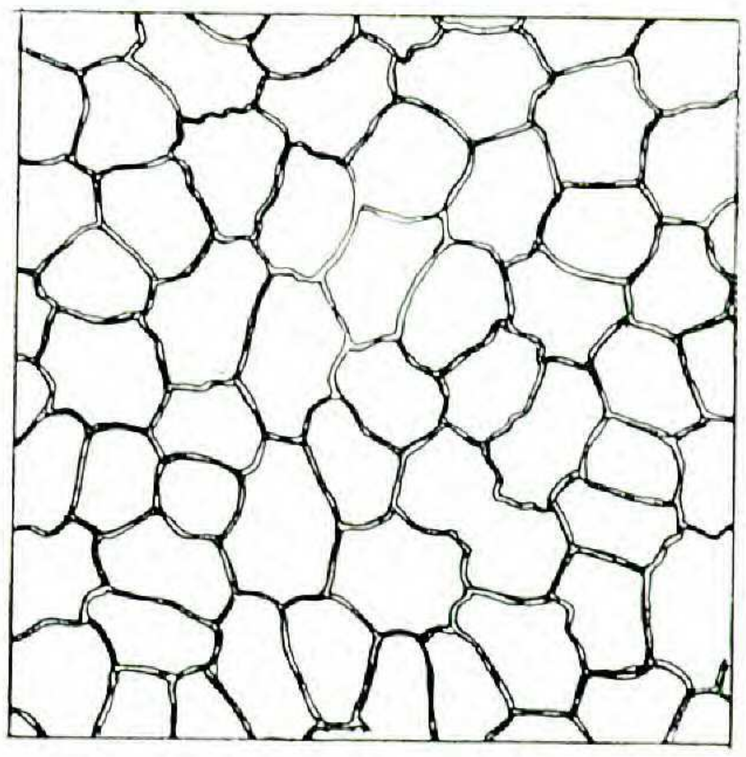
ILLUSTRATIONS OF RHEXIA SPECIES (Figs. 1—13). Showing mature hypanthium, habit sketch, seed (scale as indicated for each), sector of upper epidermis of leaf (enlarged).

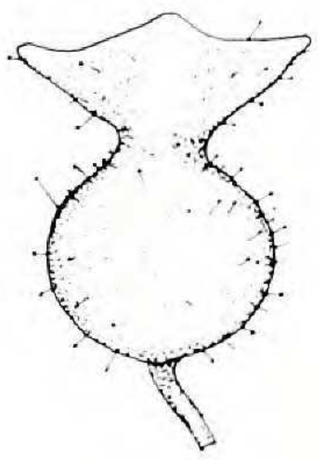


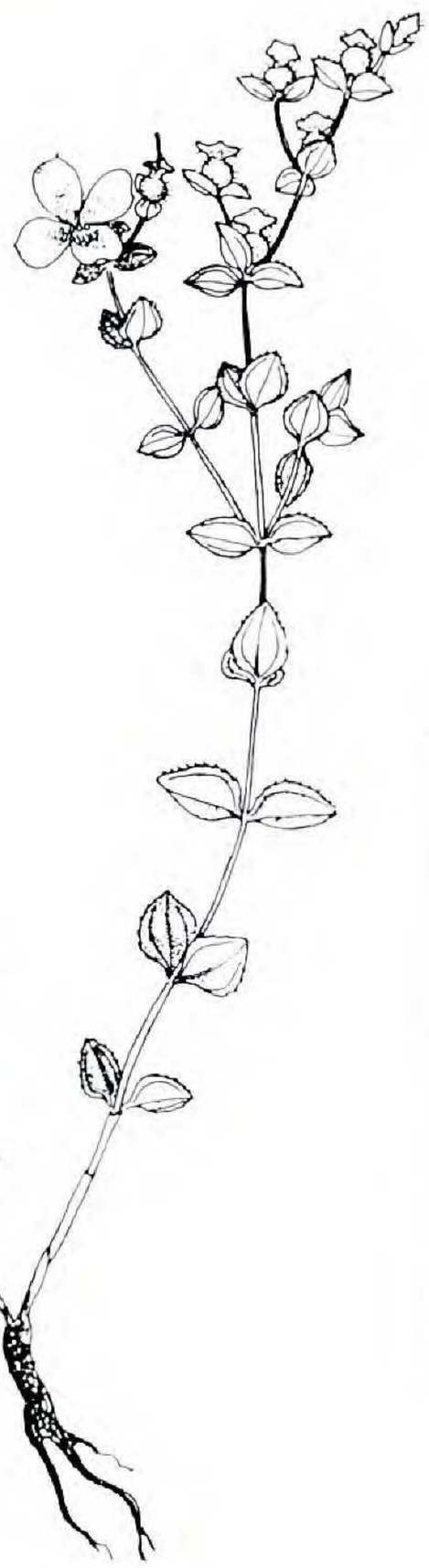


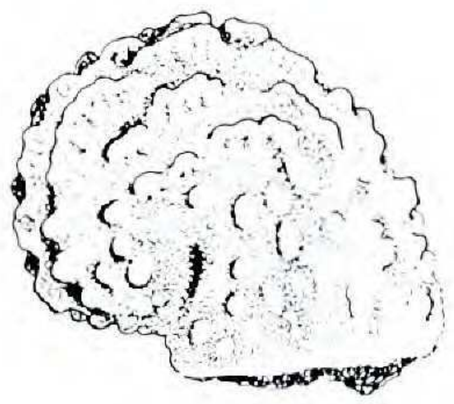




1. RHEXIA PETIOLATA (p. 400).







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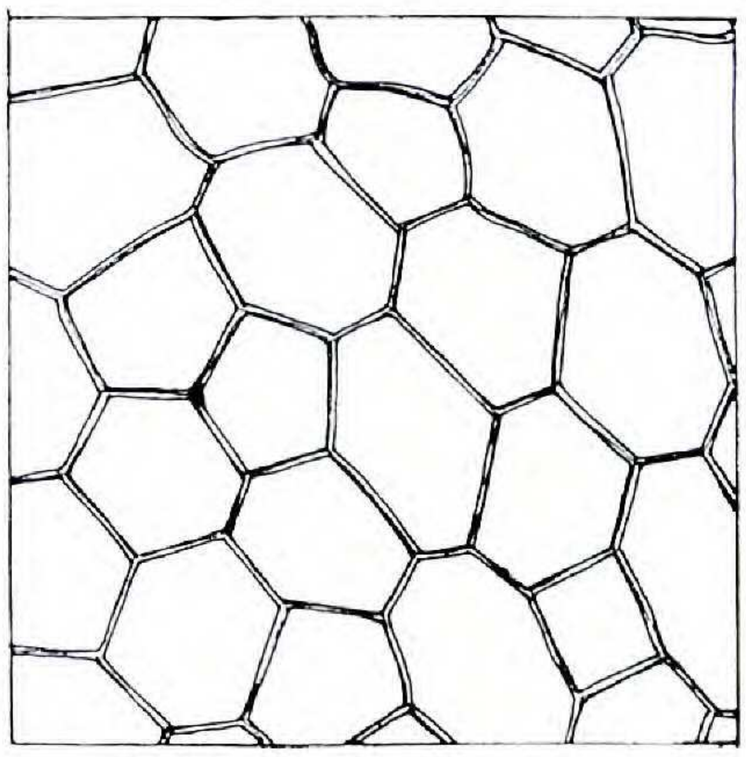
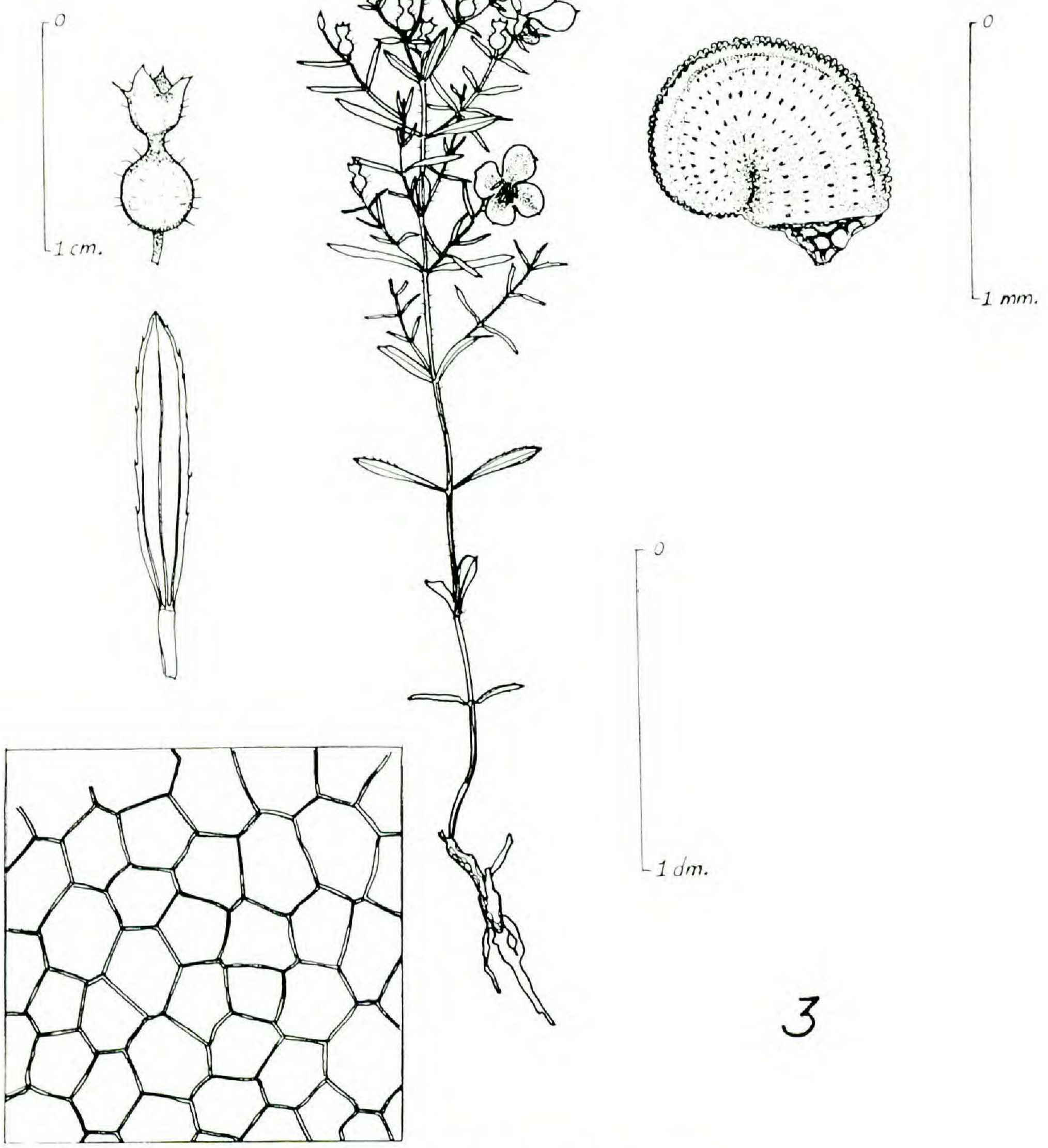
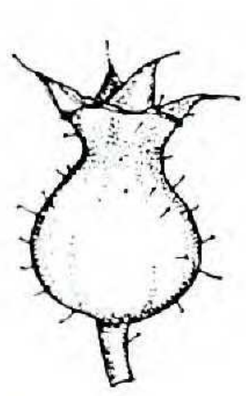
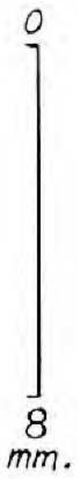


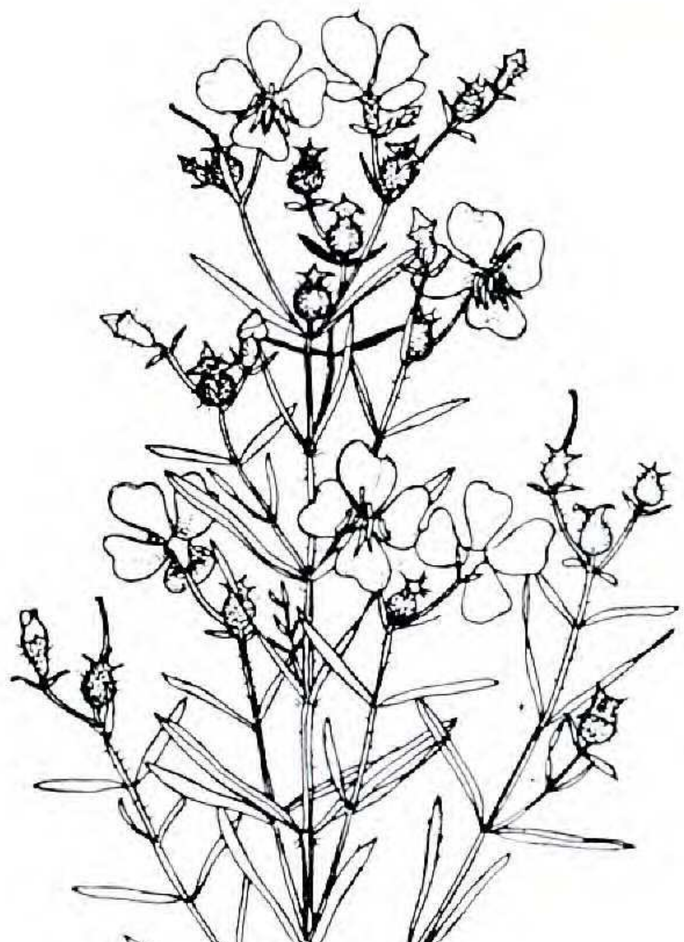
2. RHEXIA NUTTALLII (p. 401).

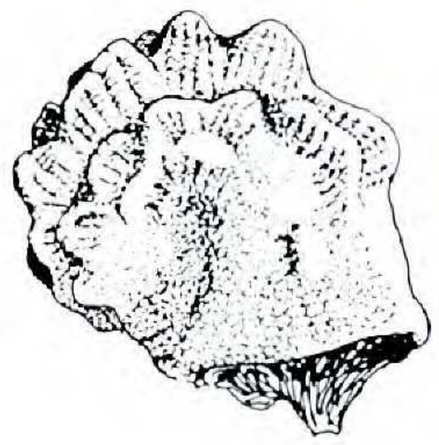


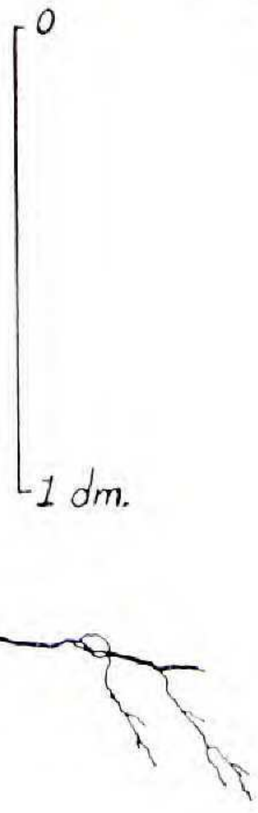
3. RHEXIA LUTEA (p. 401).

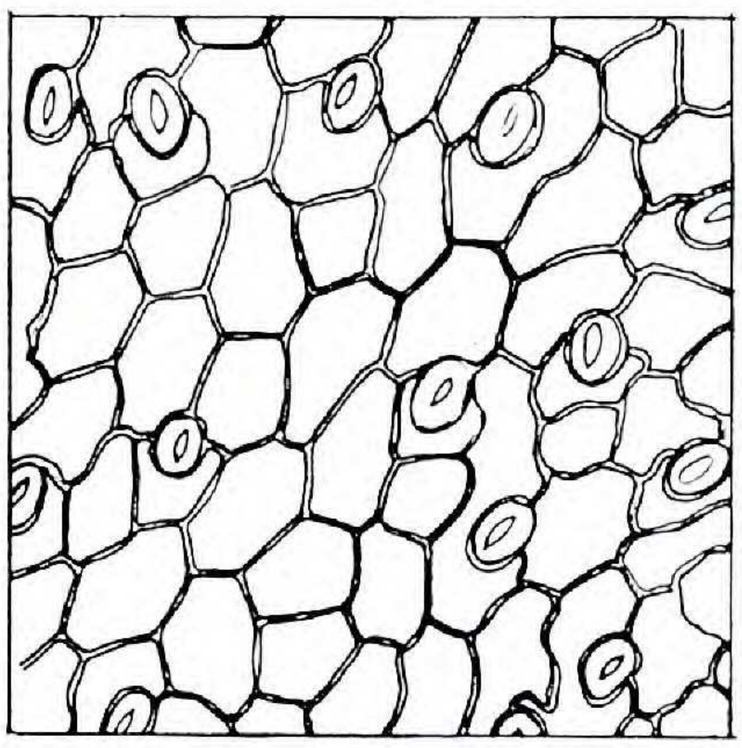












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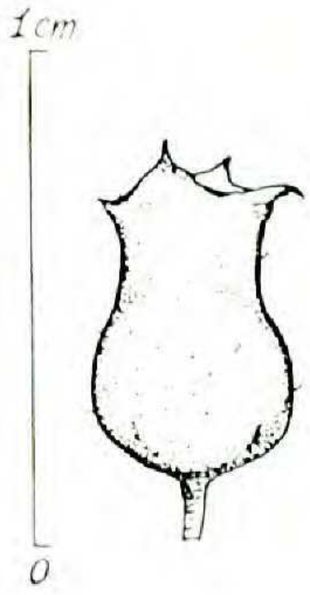
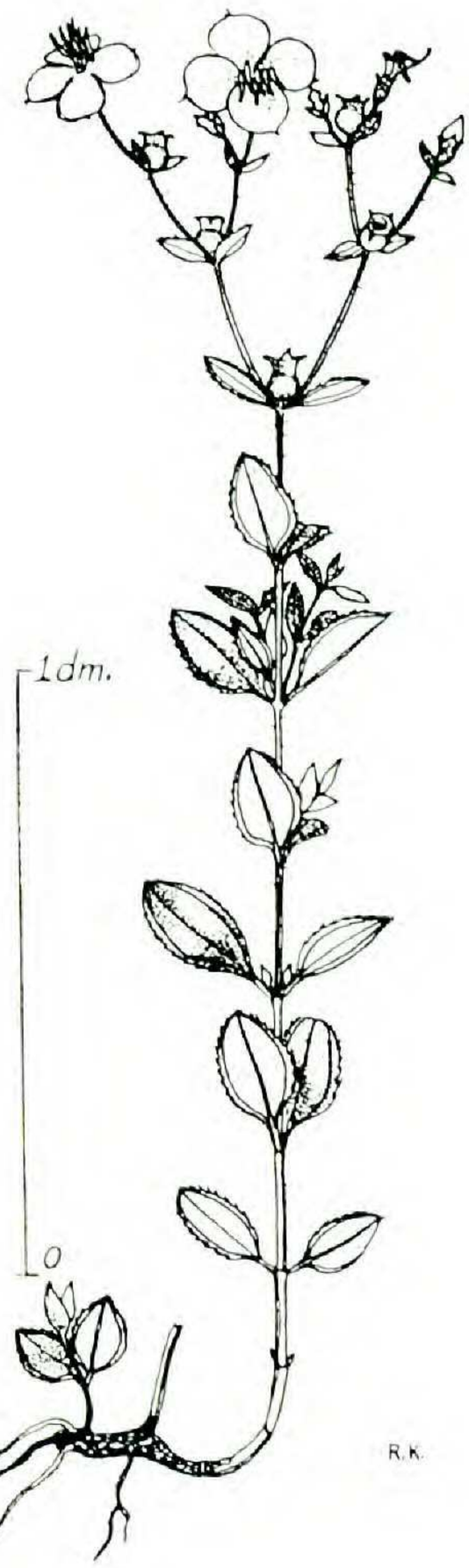
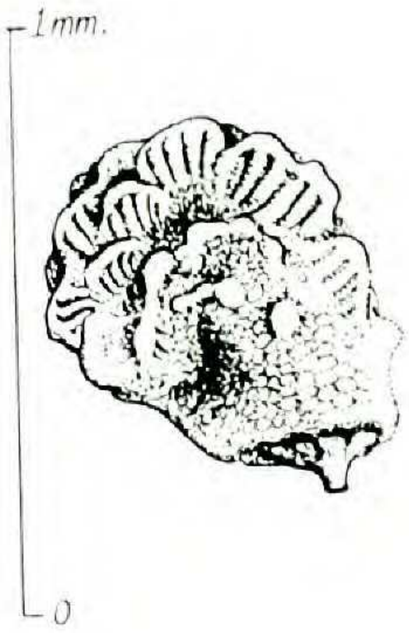
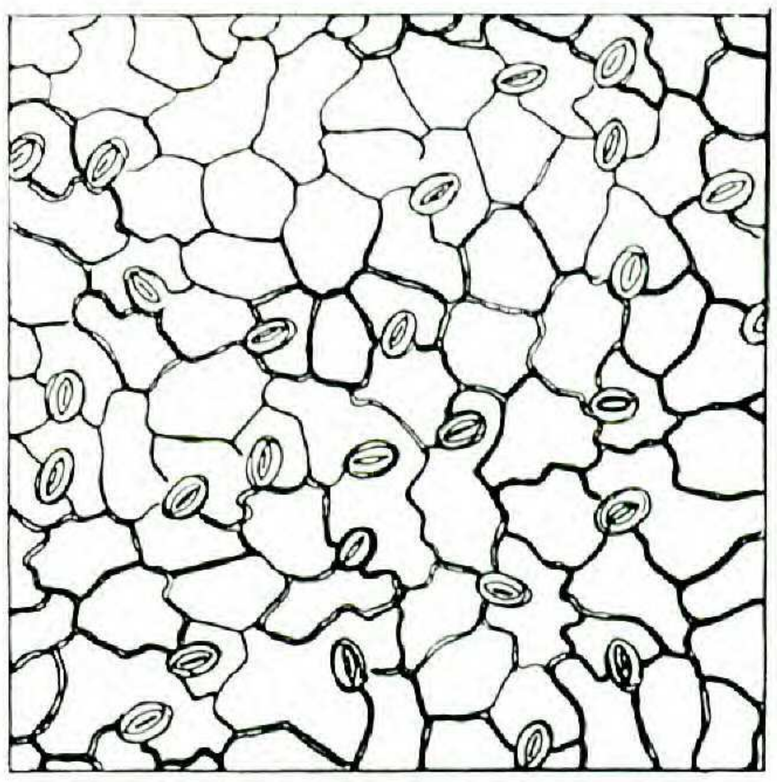
4. RHEXIA SALICIFOLIA (p. 402).









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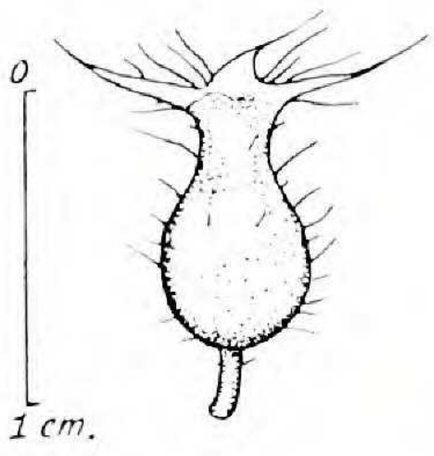
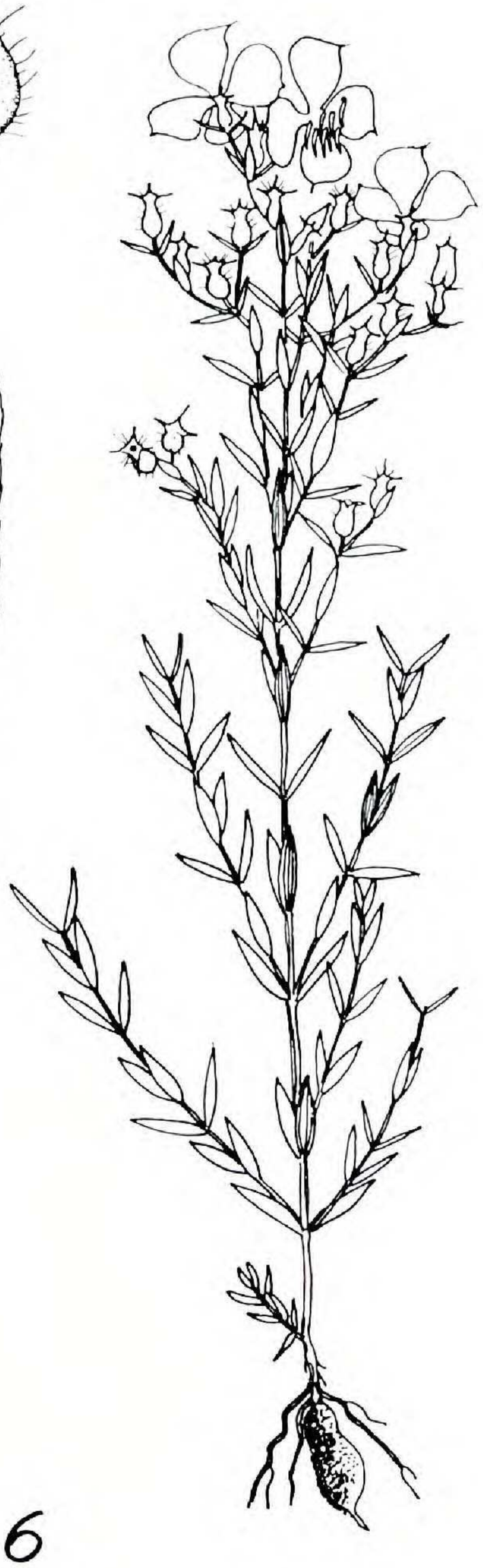
5. RHEXIA PARVIFLORA (p. 405).





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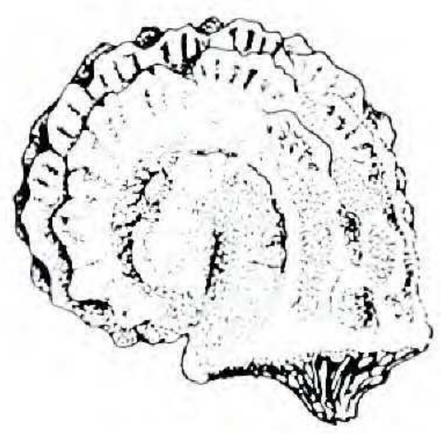
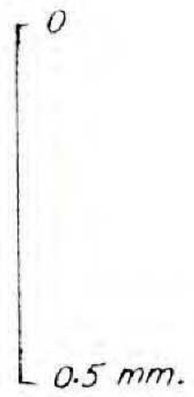
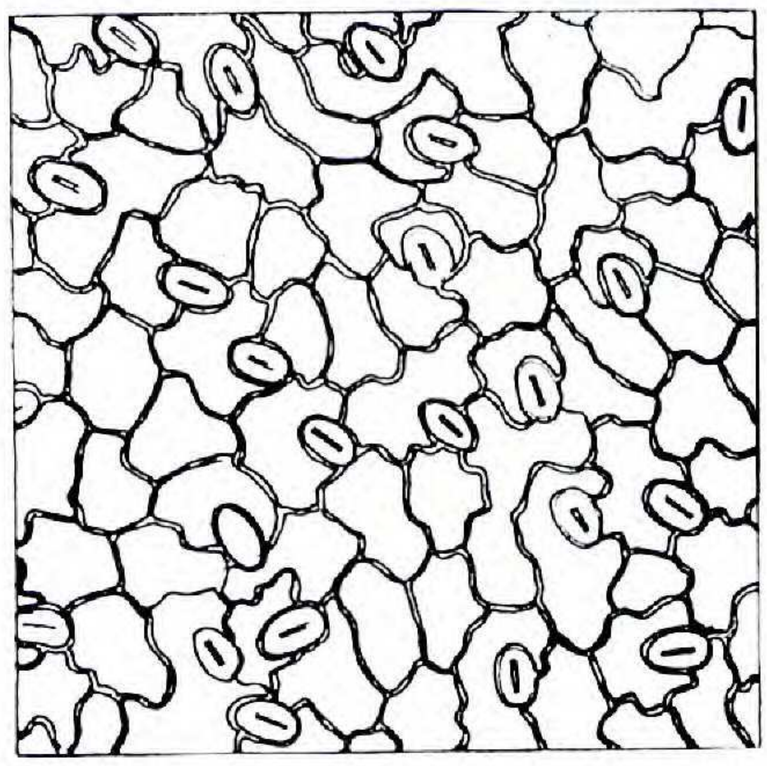
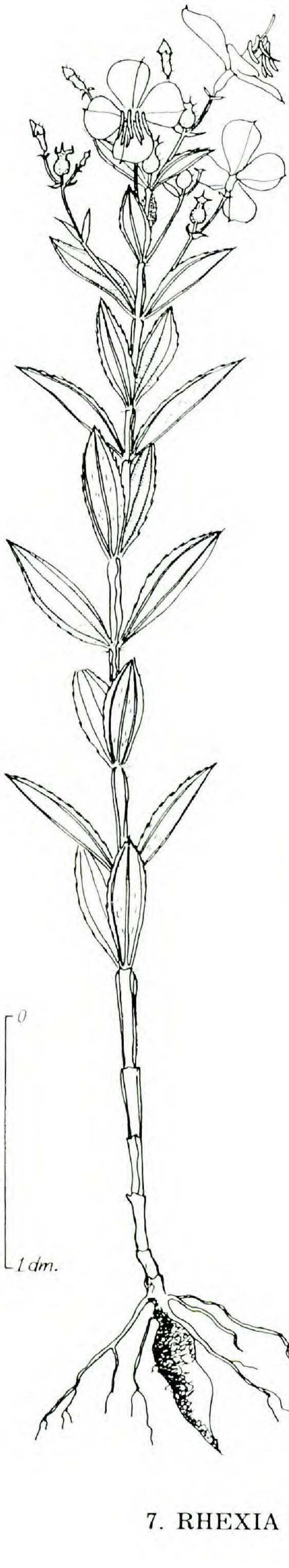
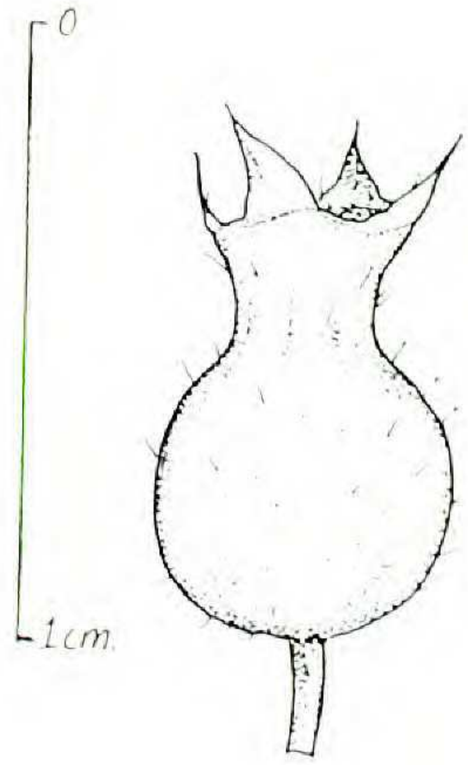


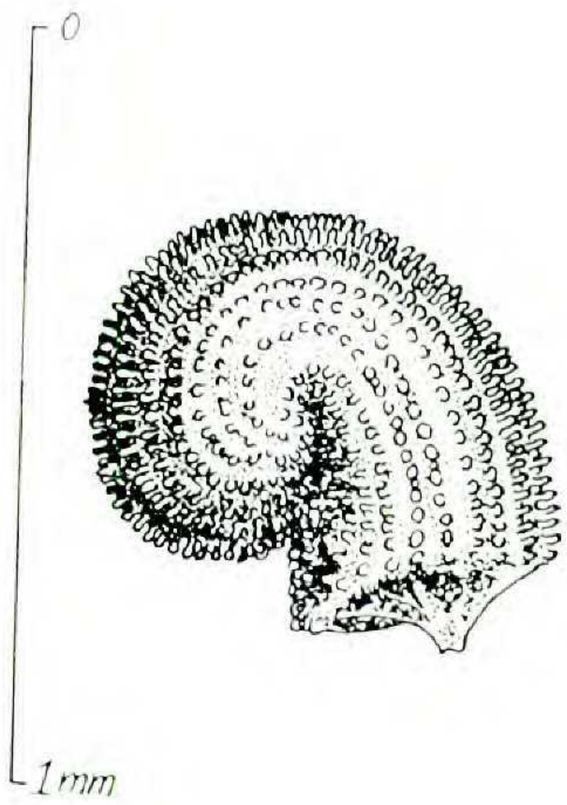


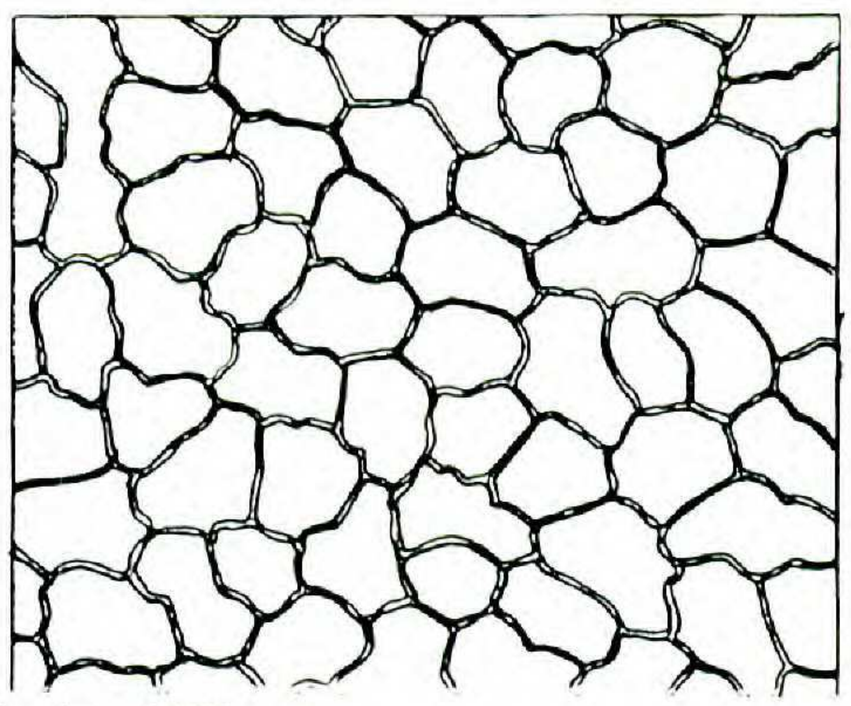


6. RHEXIA ARISTOSA (p. 406).









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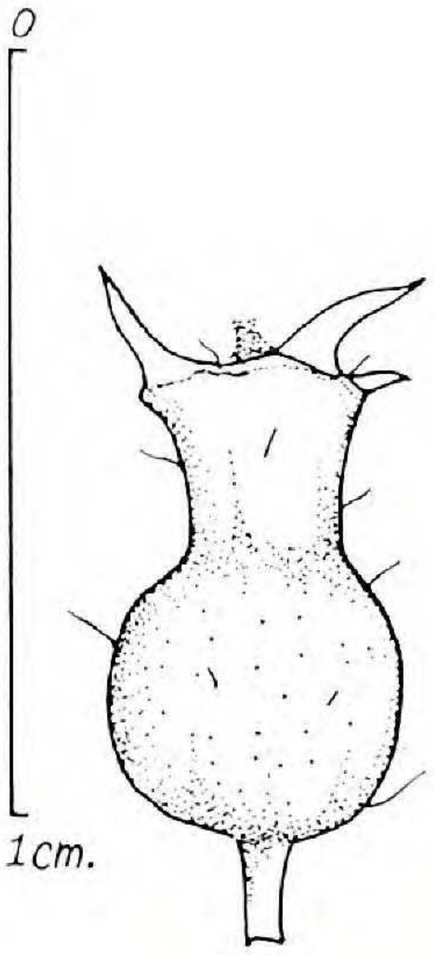
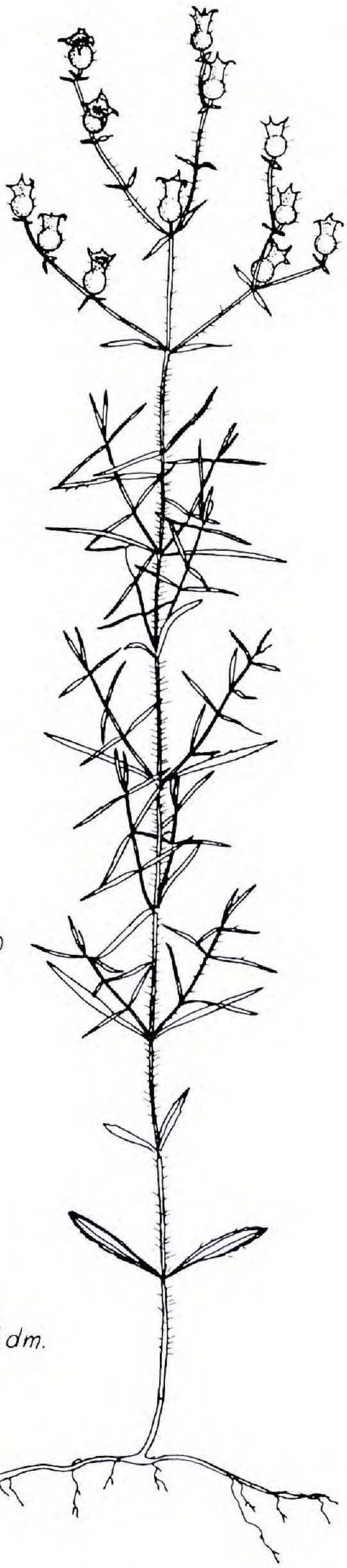
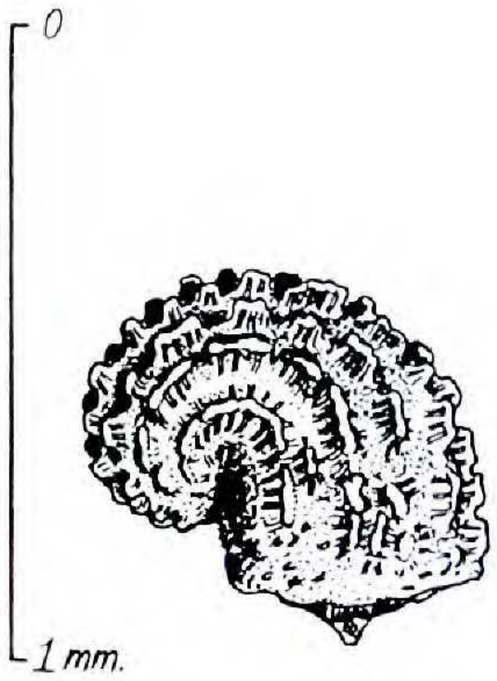
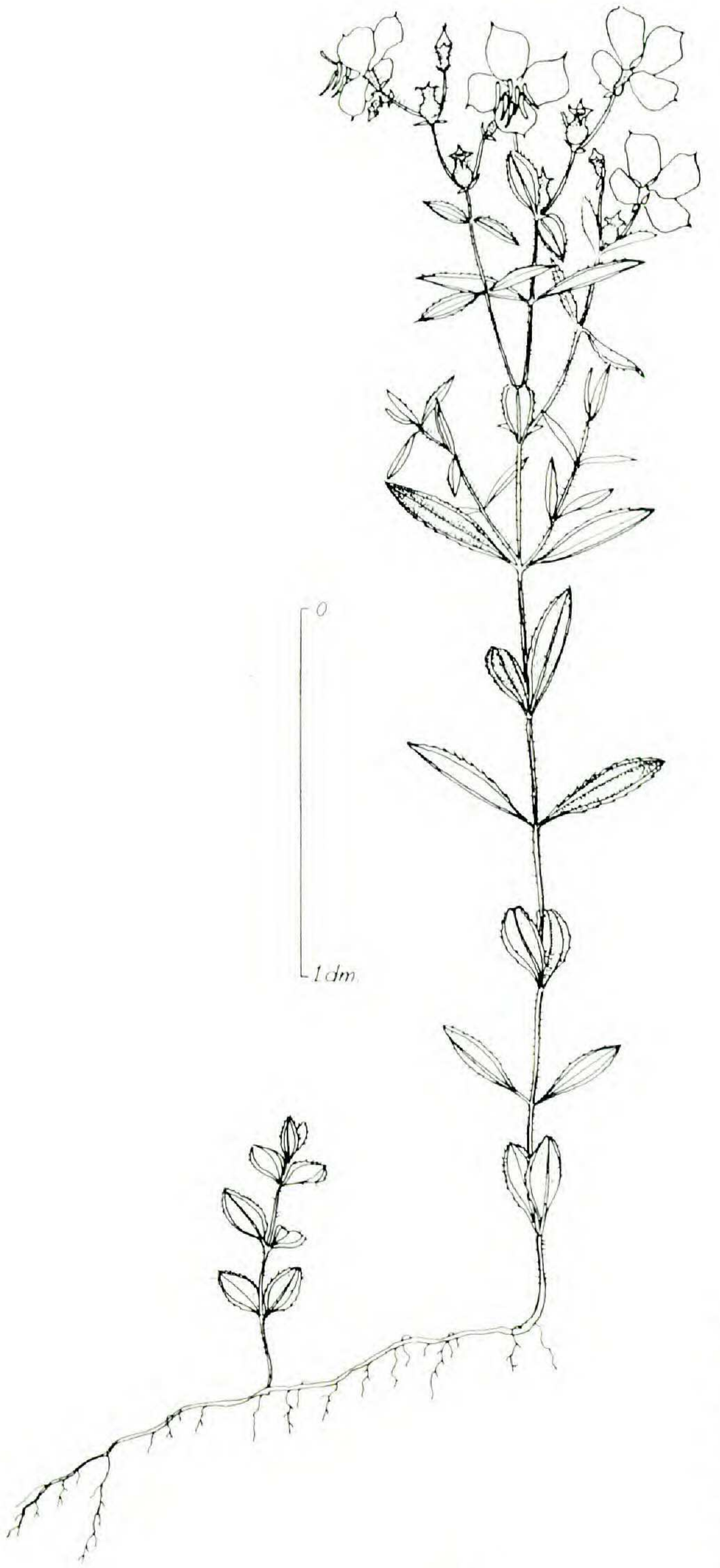
7. RHEXIA VIRGINICA (p. 407).



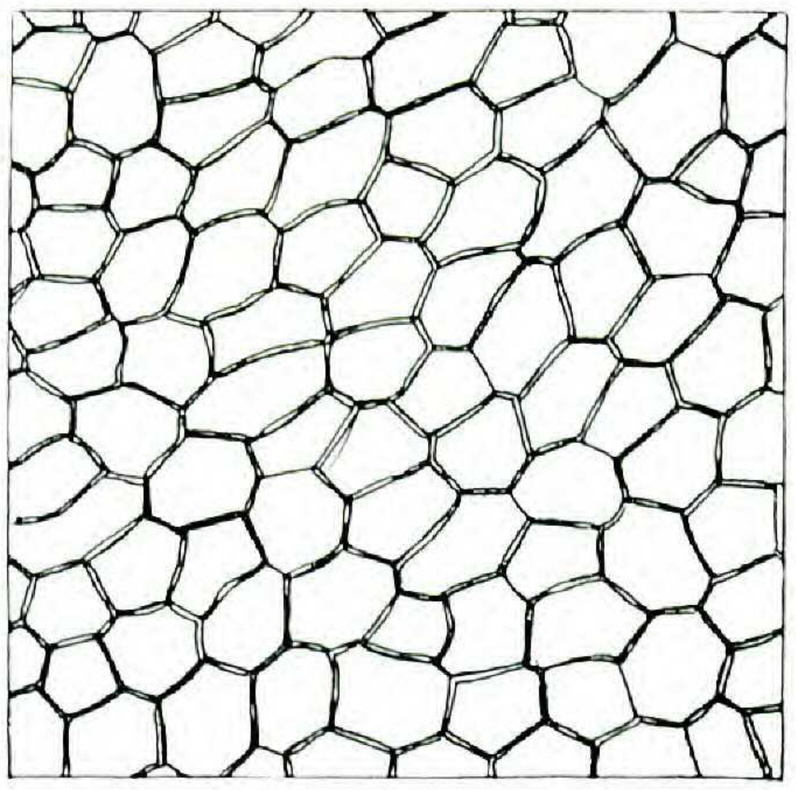




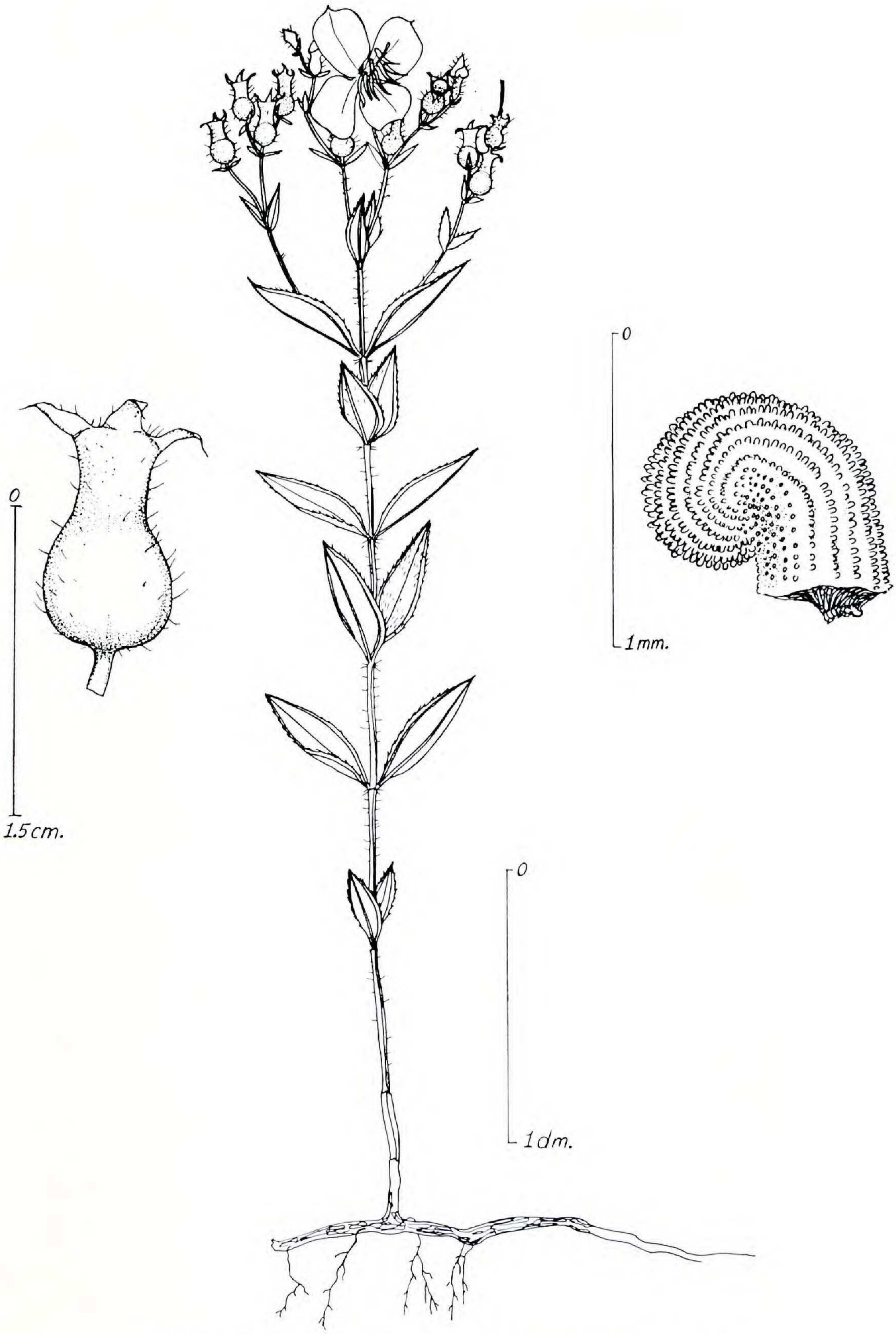
8a. RHEXIA MARIANA VAR. MARIANA, sun (narrow-leaved) plant from same clone as 8b. (p. 408).



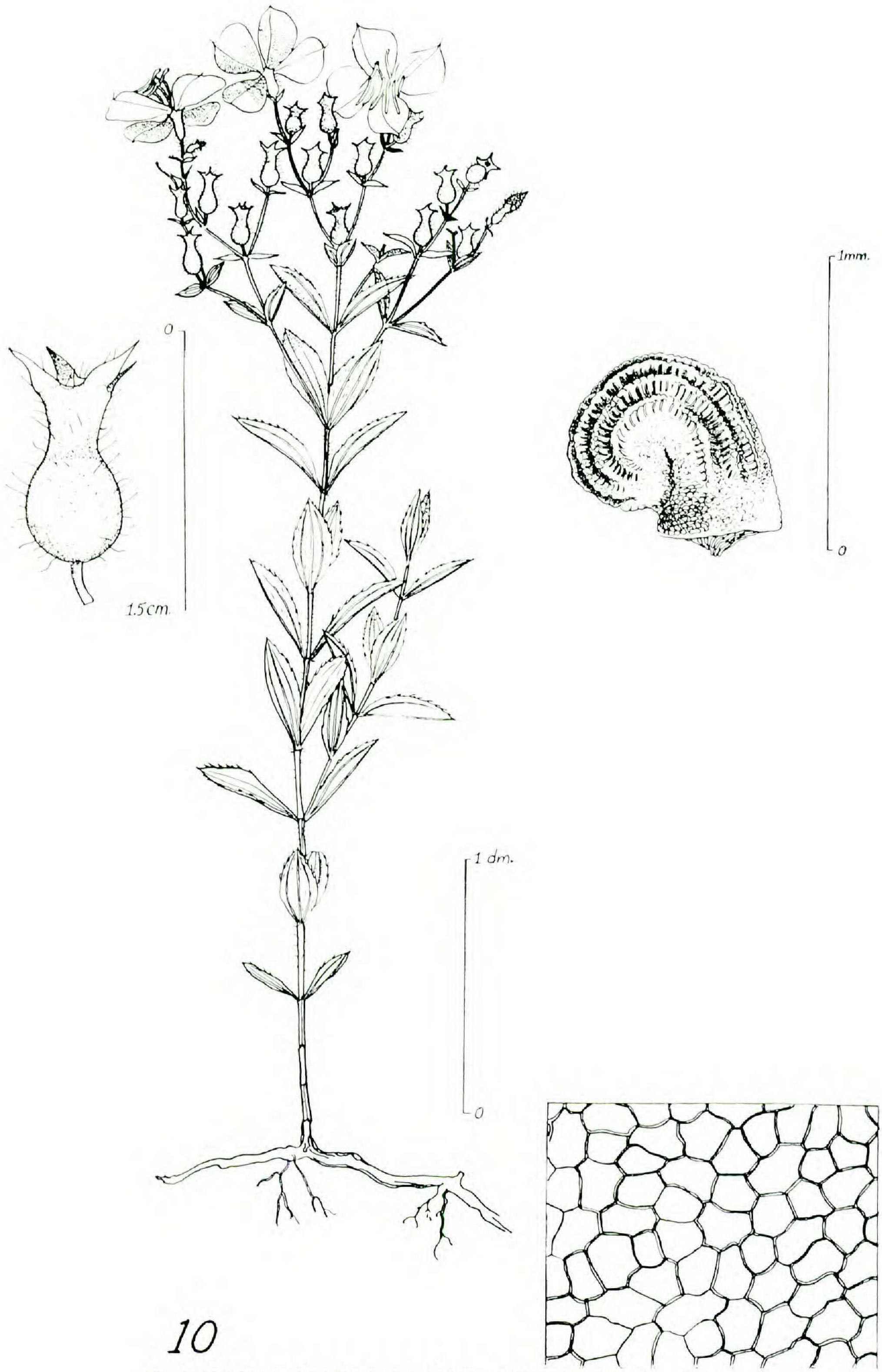
8b



8b. RHEXIA MARIANA VAR. MARIANA, shade (broad-leaved) plant from same clone as 8a. (p. 408).

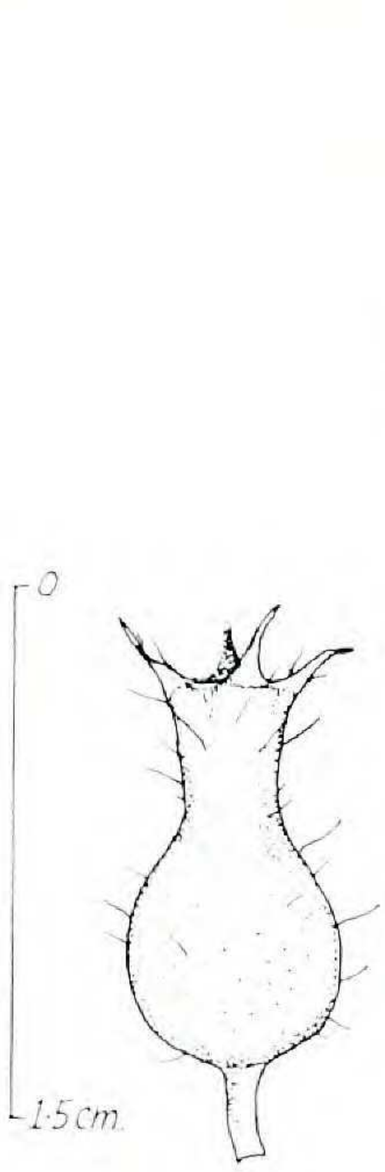


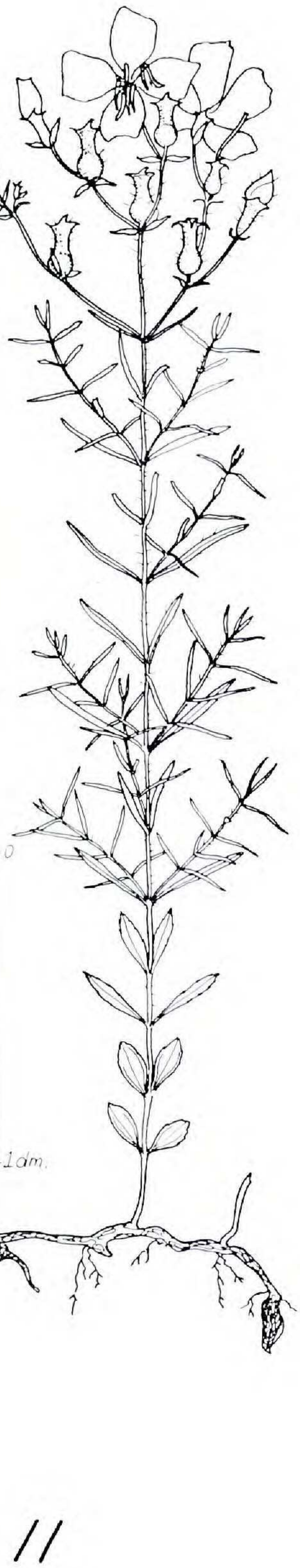
9. RHEXIA MARIANA VAR. VENTRICOSA (p. 410).

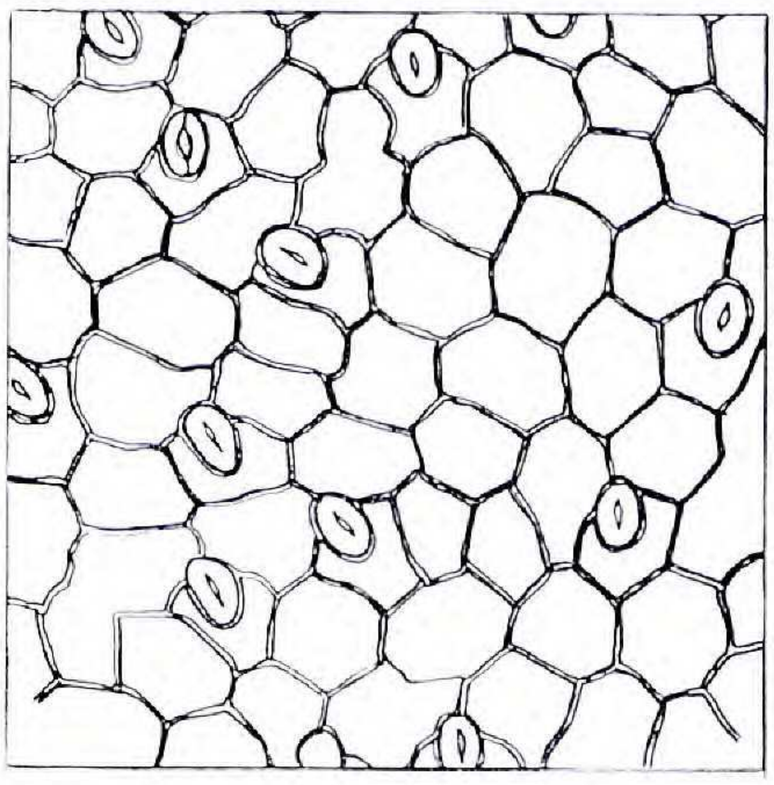


10

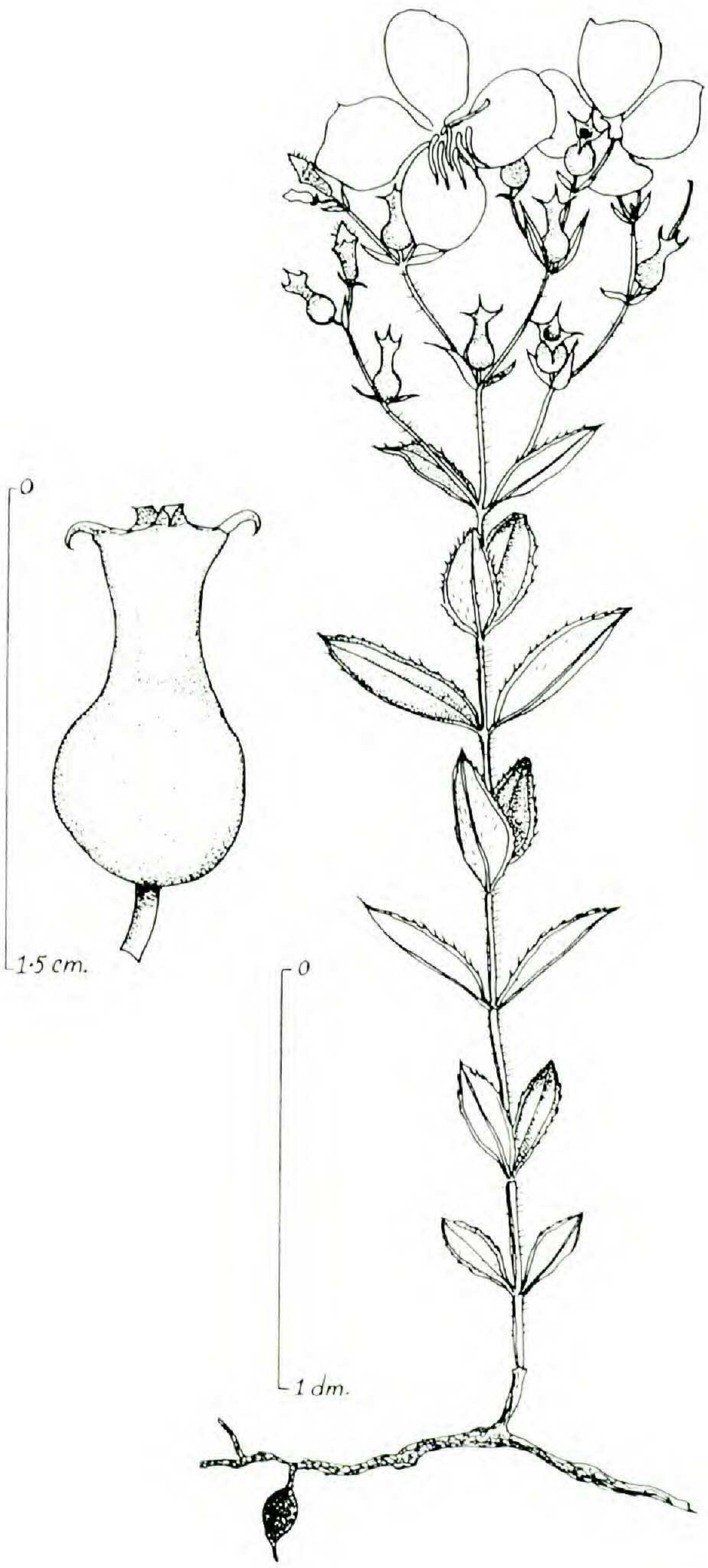
10. RHEXIA MARIANA VAR. INTERIOR (p. 410).

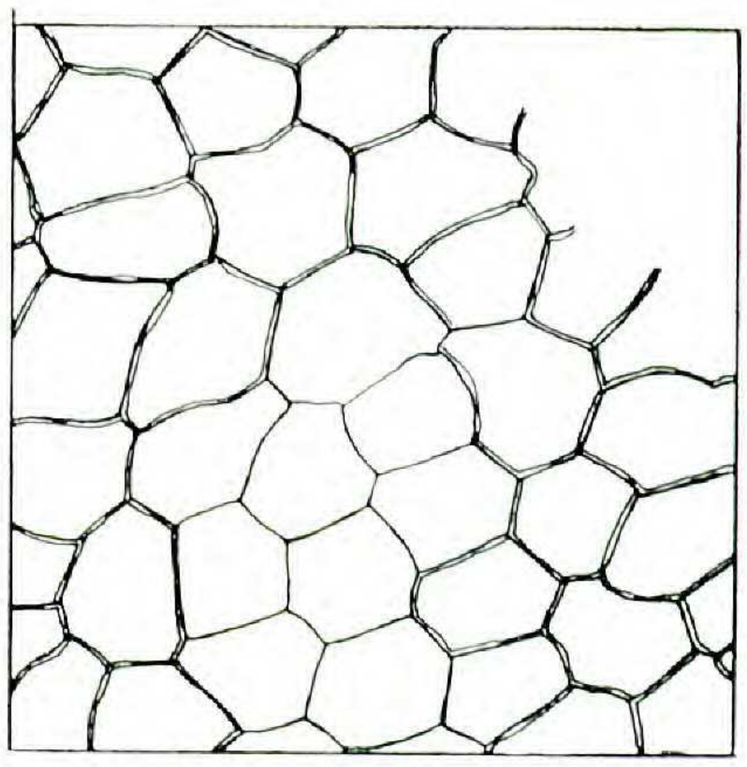






11. RHEXIA CUBENSIS (p. 411).





12

12. RHEXIA NASHII (p. 412).

13. RHEXIA ALIFANUS (p. 413).

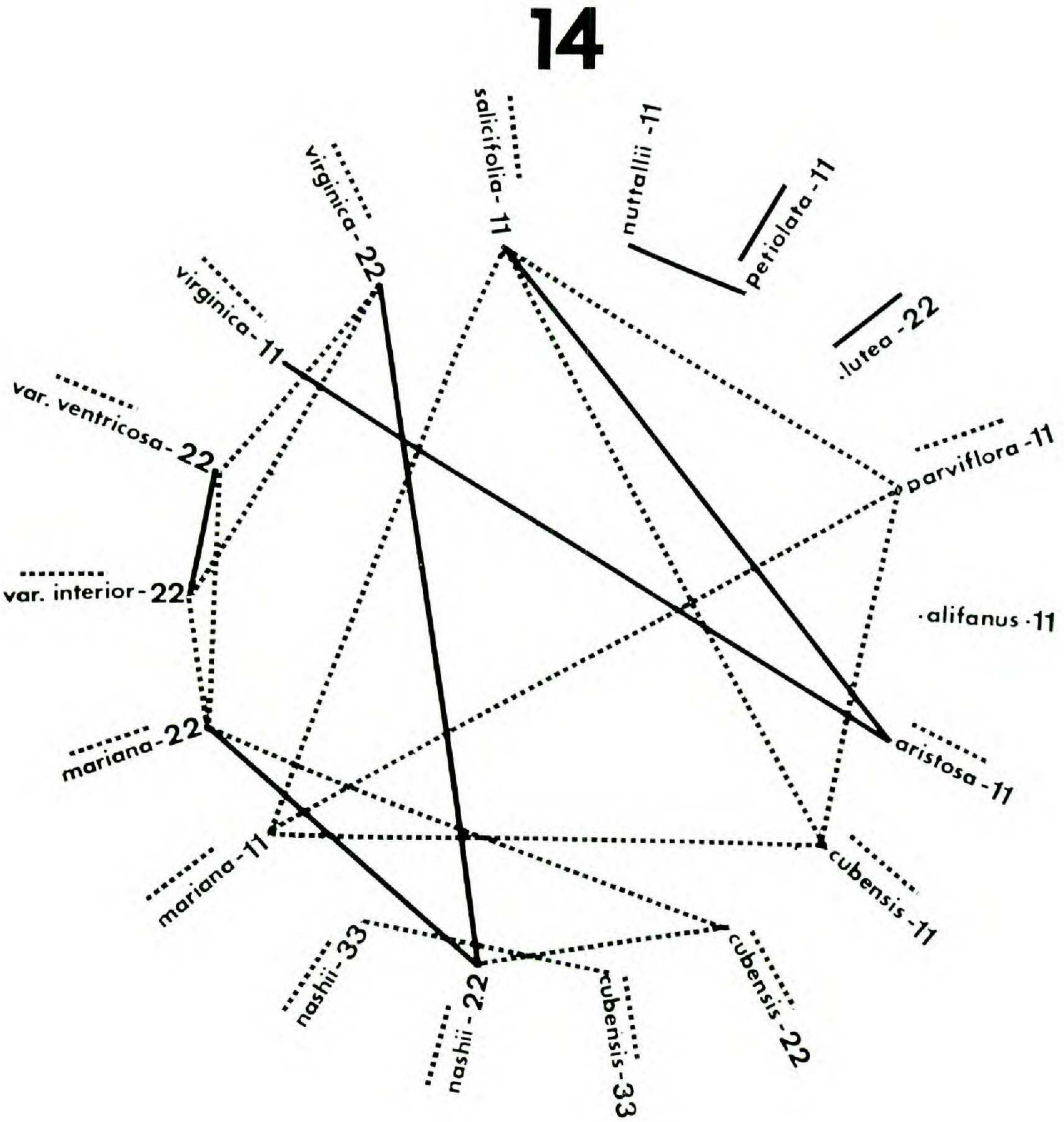
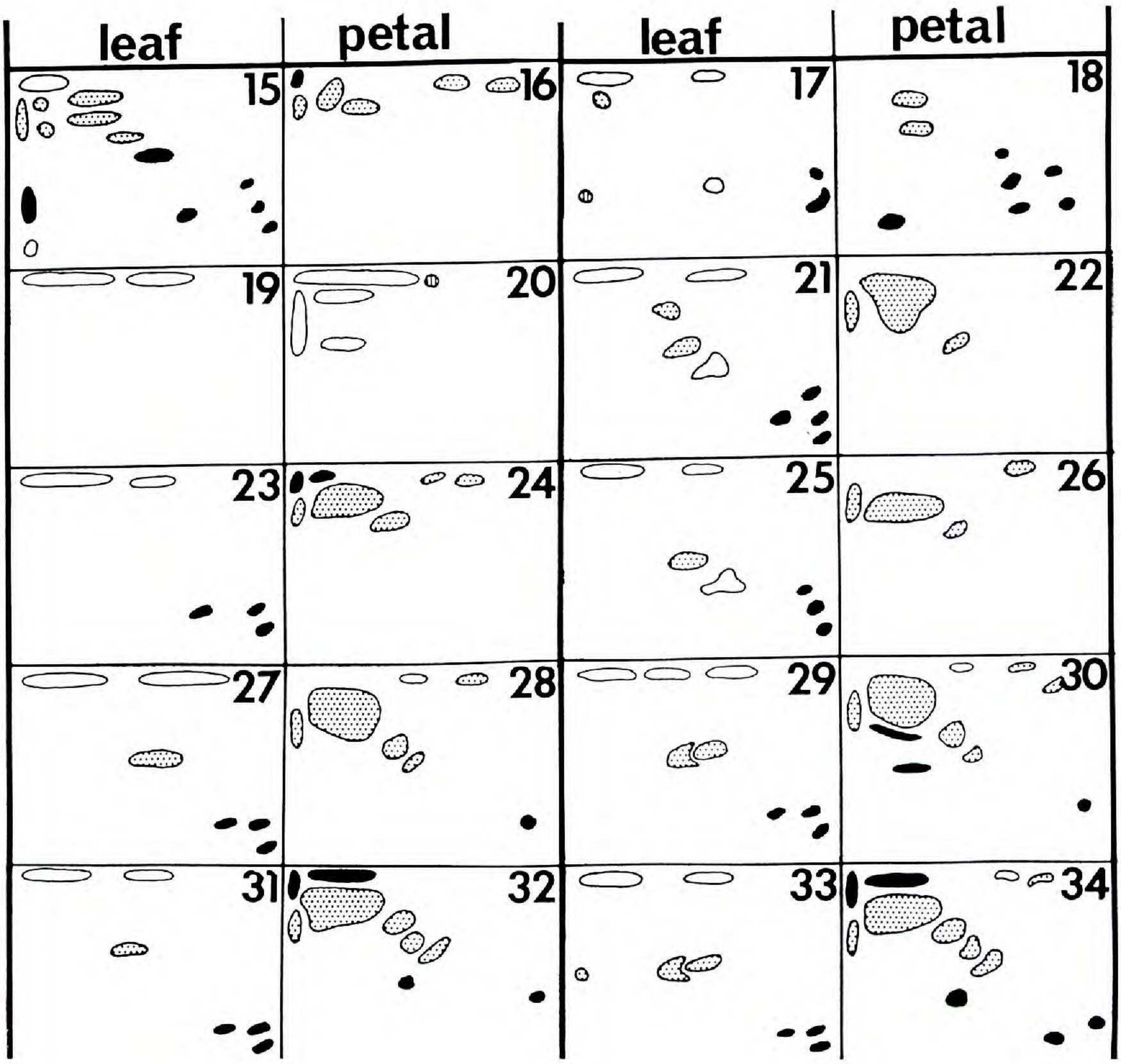
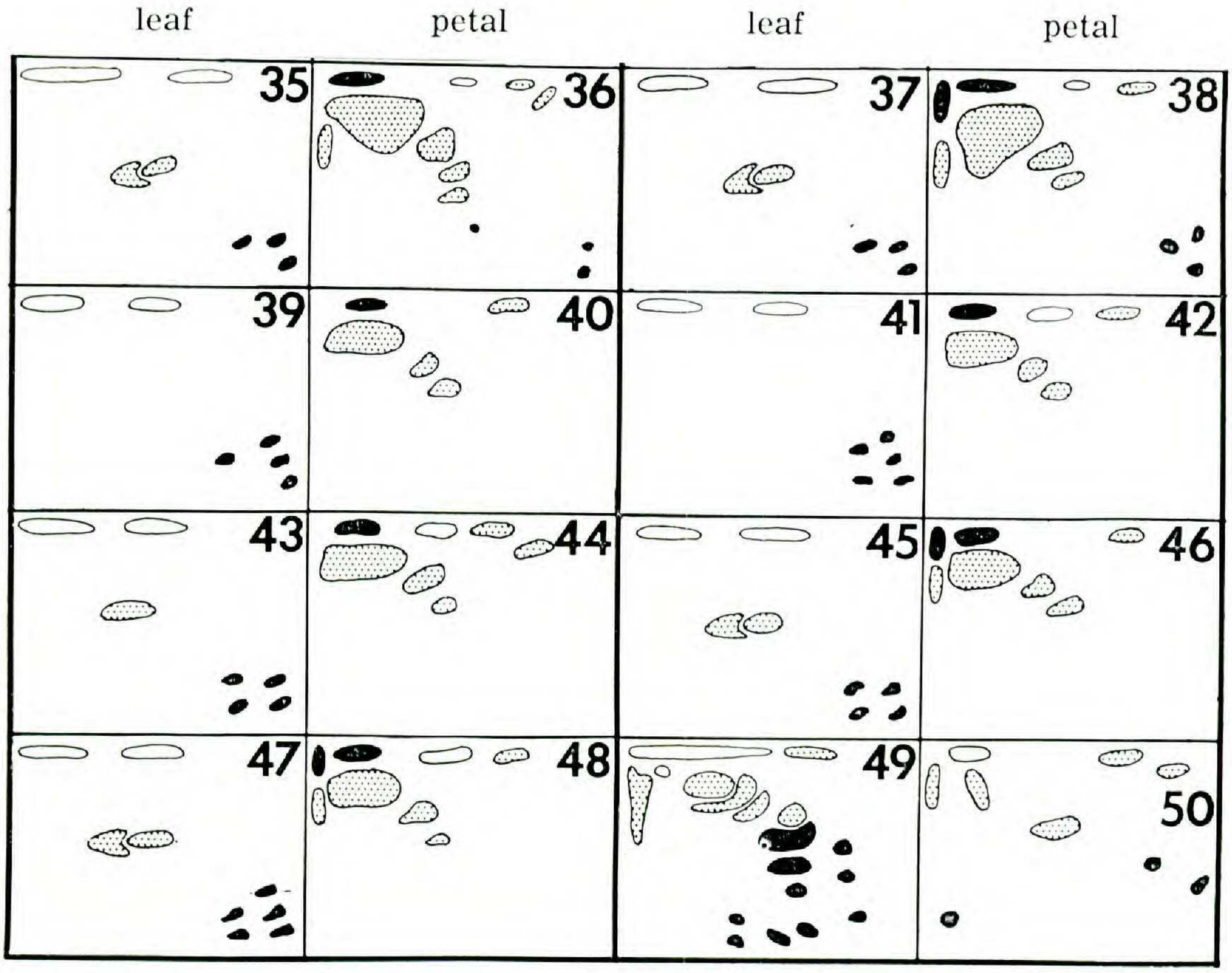


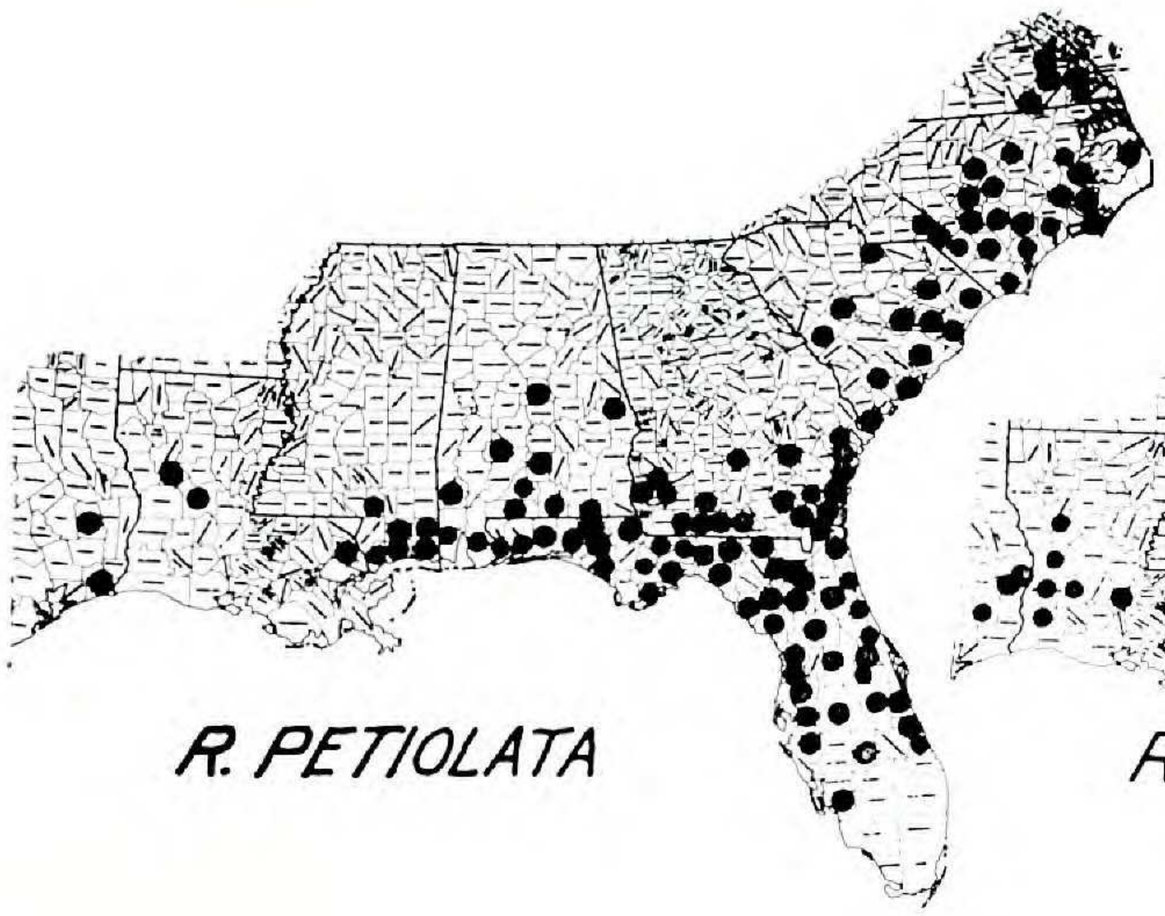
Figure 14. Artificial hybridization in *Rhexia*. Solid lines: seed formed, germinated. Dashed lines: seeds formed, did not germinate (postzygotic isolating mechanism). No connecting lines: seeds not formed (presumably prezygotic or very early postzygotic isolating mechanism). Lines above each species epithet indicate the results of "selfing," as above.



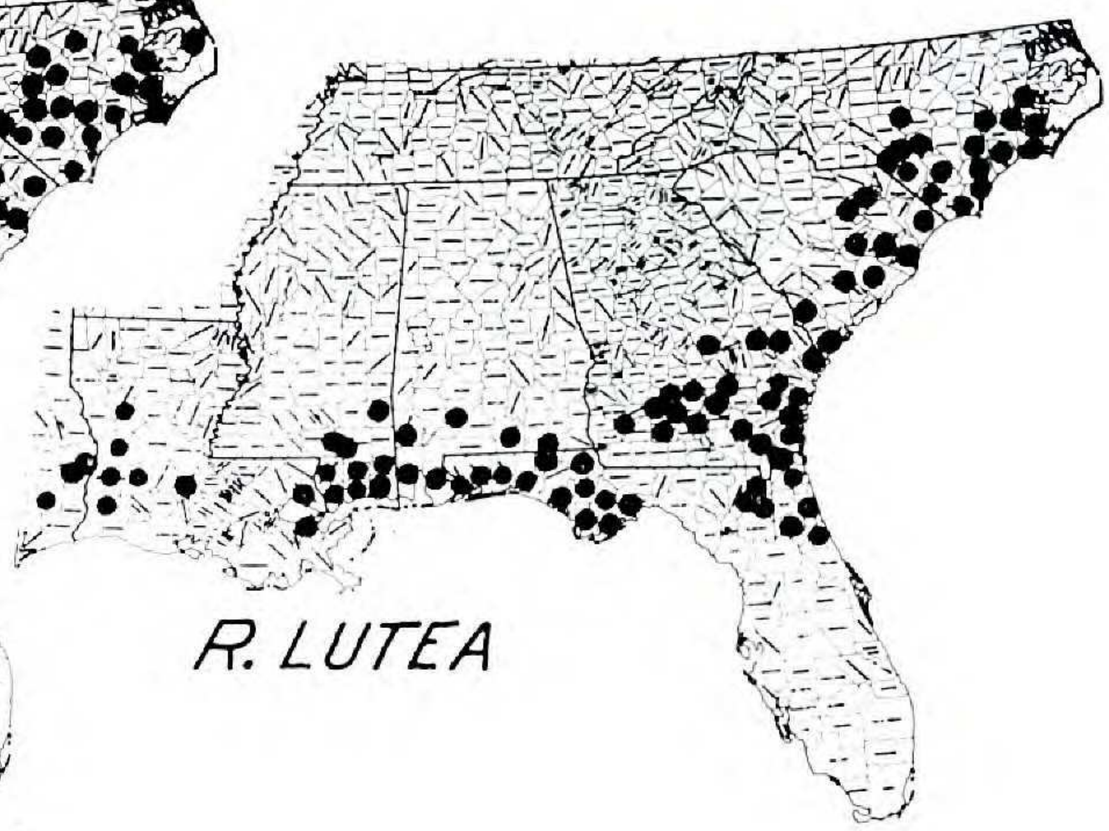
Figures 15-50. Scale drawings of *Rhexia* chromatograms as seen under ultra-violet light in ammonia vapor. Spot origin in upper left of each drawing. Open spots: yellow, dotted spots: purple, black spots: blue, striped spots: orange. Fig. 15, 16: *R. petiolata*; 17, 18: *R. nuttallii*; 19, 20: *R. lutea*; 21, 22: *R. salicifolia*; 23, 24: *R. parviflora*; 25, 26: *R. aristosa*; 27, 28: *R. virginica*, diploid; 29, 30: *R. virginica*, tetraploid; 31, 32: *R. mariana* var. *interior*; 33, 34: *R. mariana* var. *ventricosa*.



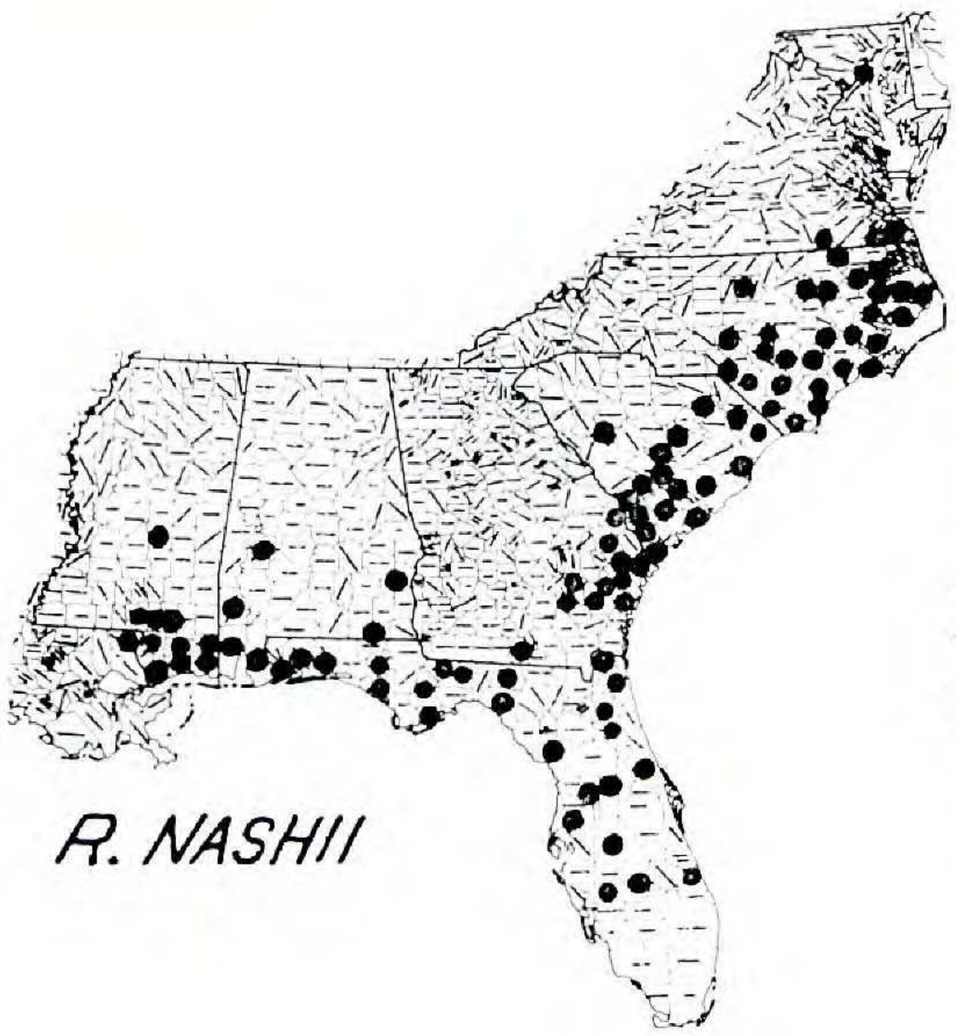
Rhexia chromatograms (continued). — 35, 36: *R. mariana*, diploid; 37, 38: *R. mariana*, tetraploid; 39, 40: *R. cubensis*, diploid; 41, 42: *R. cubensis*, tetraploid; 43, 44: *R. cubensis*, hexaploid; 45, 46: *R. nashii*, tetraploid; 47, 48: *R. nashii*, hexaploid; 49, 50: *R. alifanus*.



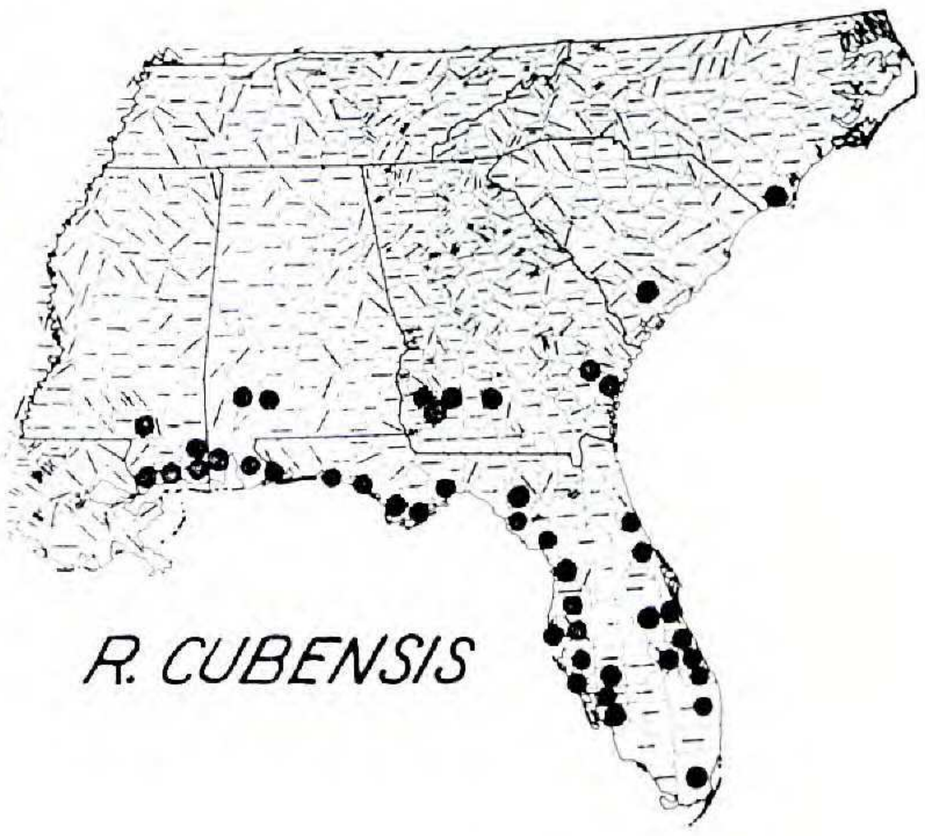
R. PETIOLATA



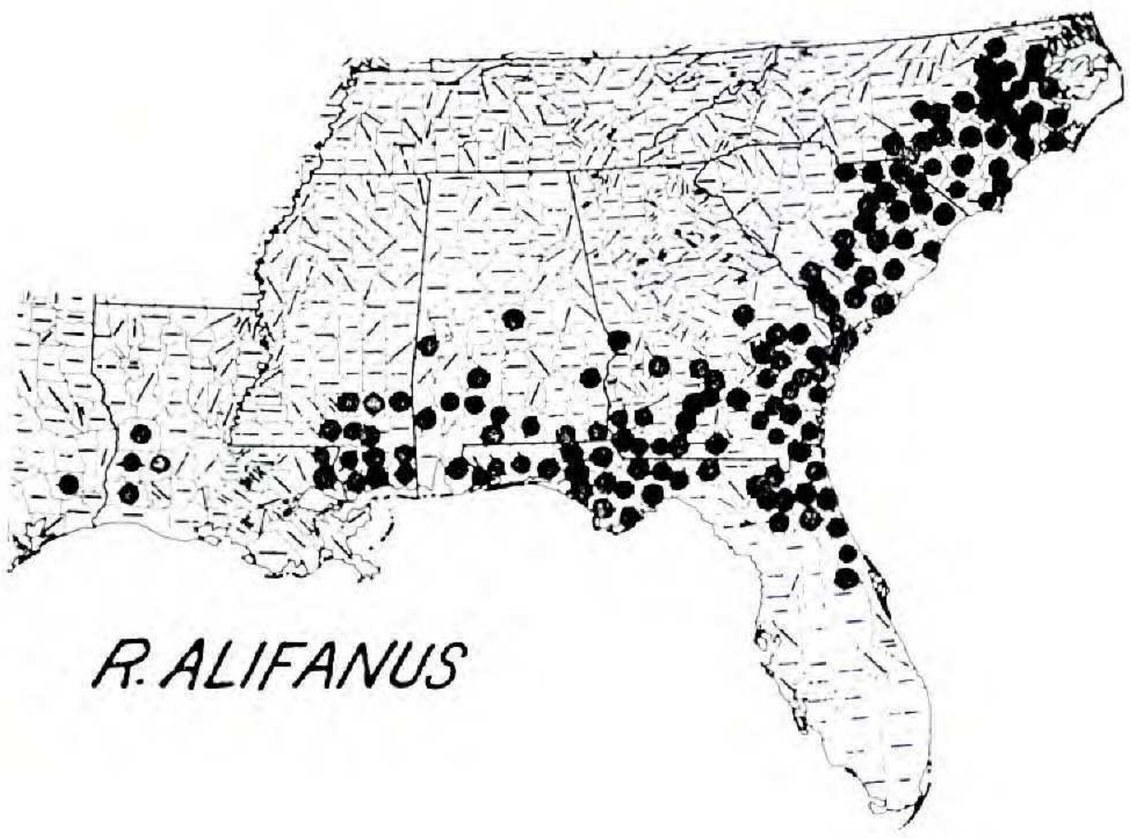
R. LUTEA



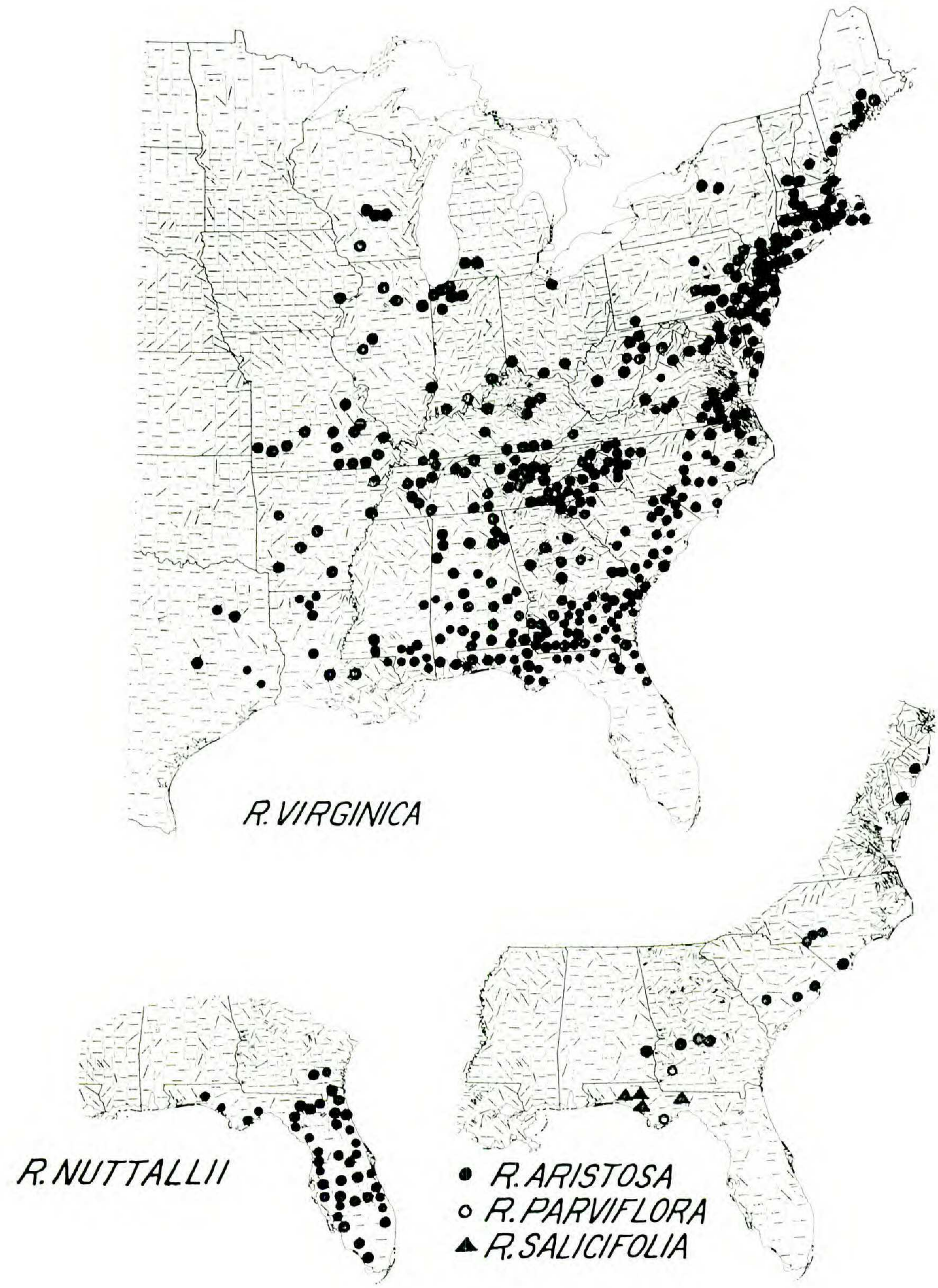
R. NASHII



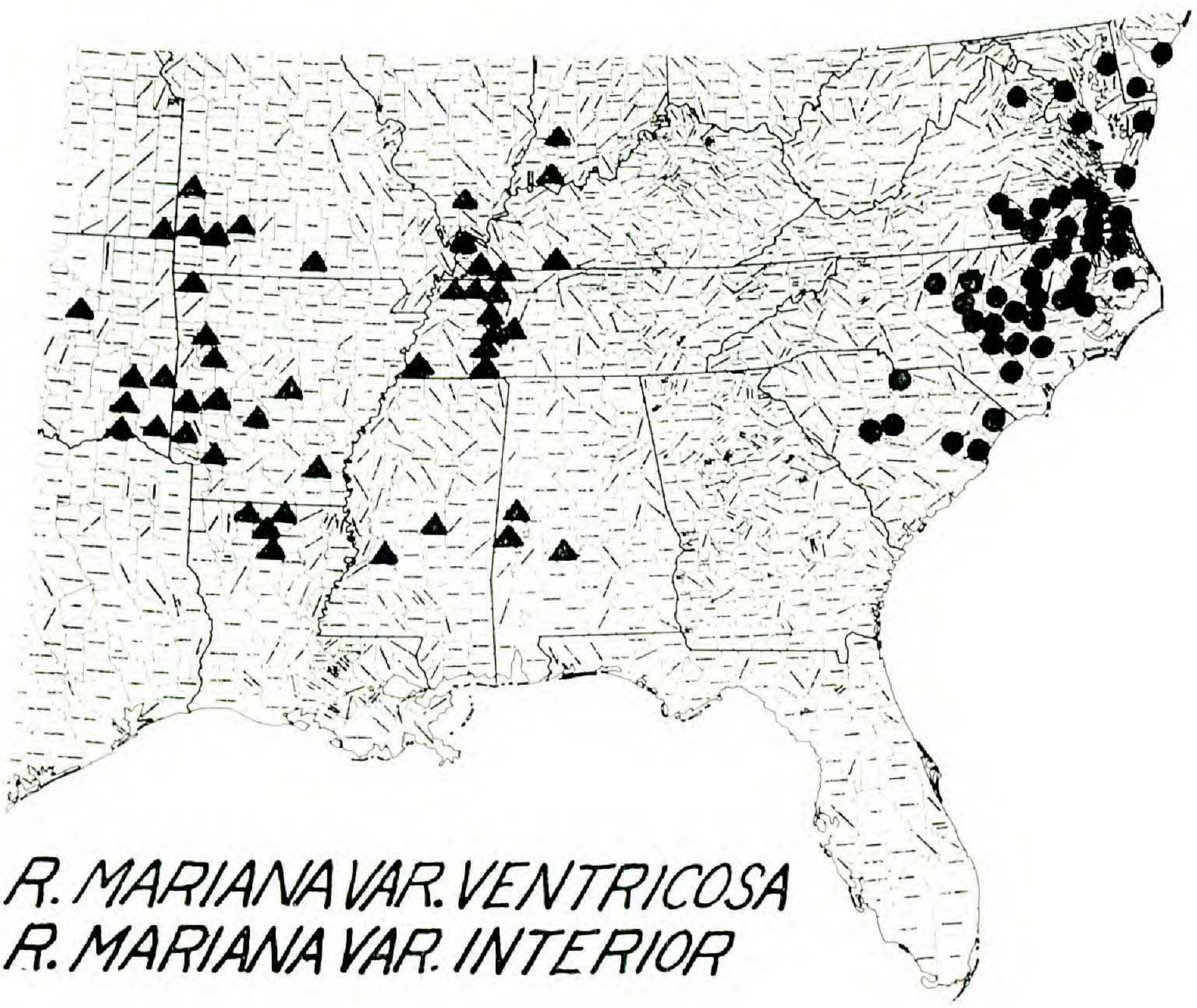
R. CUBENSIS



R. ALIFANUS


R. VIRGINICA
R. NUTTALLII
• R. ARISTOSA
○ R. PARVIFLORA
▲ R. SALICIFOLIA

R. MARIANA VAR. MARIANA


○ R. MARIANA VAR. VENTRICOSA
△ R. MARIANA VAR. INTERIOR